SUSTAINING BIODIVERSITY CONSERVATION IN AND AROUND NYUNGWE NATIONAL PARK (NNP)

Trends in Populations of Birds and Mammals in Nyungwe National Park, Southwest Rwanda

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EXECUTIVE SUMMARY

1. This report describes the results of monitoring efforts at Nyungwe National Park between 1997 and 2011. Although data extend back to 1995 Maisel (in litt.) suggests that early data had idenitification errors, especially for birds. Data were examined for trends in abundance and distribution of 15 medium and large mammals, including primates, squirrels and terrestrial mammals. We also examined 193 bird species for trends in density, relative abundance, and species richness over time and trends in distribution by elevation. In addition to general trends, we asked how well the mammal data could be used to inform us about the effectiveness of park patrolling and whether changes in in bird communities informed us about climate change.

2. Mammals were sampled using line transect and distance sampling methods for primates and squirrels and by sign surveys for terrestrial mammals. Sampling resulted in more than 3,000 mammal observations. Birds communities were sampled using variable point counts and resulted in more than 82,000 observations.

3. Changes in sampling over time resulted in changes in the distribution of effort by elevation, changes in the temporal pattern of sampling and changes in the spatial extent of sampling. We used a number of methods to control for spurious results attributable to sampling differences over time. These included use of missing data for occupancy analysis, lumping sampling by year and using sampling effort as a covariate for mammals, and splitting data into a 1997-2011 data set and a 2005-2011 dataset.

4. Primate distribution in the study area has generally declined over time with the exception of Angolan colobus monkeys. Declines in distribution range from 12% for Mona monkeys to 40% for chimpanzees. Primate densities have remained relatively stable over time except for a decline in density of Grey-cheeked mangabeys and an increase in density of Mona monkeys.

5. Distribution of Boehm's squirrel, Montane sun squirrel and Cuvier's fire-footed squirrel declined over time between 15% and 57%. Densities of all species declined until 2005 and have since started to increase again.

6. Terrestrial mammals, including three duiker species, brush-tailed porcupine and giant pouched rat all declined in distribution between 4% and 27%. Bushpigs, however, showed an increase in distribution over time by almost 20%. We were unable to estimate densities of terrestrial mammals due to lack of direct observations.

7. We have some evidence that patrols initiated in 2003 have been effective in curbing declines in mammal populations. Although the distribution of mammals is generally declining, primate population densities have remained relatively stable, and squirrel populations are on the increase. Bushpig distribution (and presumably abundance) is also increasing. Other terrestrial mammal populations however, continue to decline, most likely due to hunting.

8. We observed 208 species detected along the original 10 transects and surveyed between 1997 and 2011, and 161 species along the additional10 transects established in 2005. Average annual species richness was estimated as 115 species (± 9) present along the original 10 transects in a

given year. For the transects established in 2005, average annual species richness was 125 ($\pm$ 9) species per year. The higher species richness was attributed to additions of new habitats in 2005. Similarity in species composition was high in all years and between datasets, indicating stable bird communities in both sets of transects.

9. For the 1997-2011 surveys, we observed 193 species, excluding species that were only observed flying overhead. We estimated density and relative abundance (encounter rate) for 78 species that had at least 5 years of non-zero data. Annual correlations between density and relative abundance were acceptably high (mean = 0.78) and we used relative abundance to extend analyses of elevation trends to 108 species. For the 2005-2011 surveys, we observed 157 species (excluding flying birds) and estimated density and relative abundance for 97 species with at least 5 years of non-zero data. Again, Annual correlations between density and relative abundance were acceptably high (mean = 0.78).

10. Eighteen species, including 6 Warblers, 3 flycatchers, and 3 sunbirds exhibited trends in density between 1997 and 2011. Sunbirds and flycatchers were increasing in abundance at low and high elevations, whereas warblers did not show consistent trends. Densities of turacos were declining at lower elevations and trogons were increasing.

11. Increases in the altitudinal distribution of birds are often attributed to warming climates. For 92 species observed between 1997 and 2011, we made priori predictions as to whether we expected no trends in mean elevation of observations over time (27 species) or we expected an increase in mean elevation of observations over time (65 species). We found that 23 species showed declining trends in mean elevation, 44 species showed no trend in mean elevation, and 25 species showed increasing trends in mean elevation. Significantly more species exhibited no change in mean elevation than expected and species increasing with increasing trends in elevation were not significantly different from a random sampling. We conclude that there has not been a strong response by species expected to be sensitive to climate change. Within species groups, the strongest response was by small-bodied sunbirds, tits and warblers.

12. We conclude that bird communities sampled in the 1997-2011 and 2005-2011 samples have shown strong stability in species richness over time, and that on average, abundance and elevation distribution has remained relatively constant. We find little evidence for impacts of climate change, except for increasing elevation trends for some small-bodied bird species.

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INTRODUCTION

Nyungwe National Park, in southwestern Rwanda (2°15' – 2°55' S, 29°00'– 29°30' E), is one of the most biologically important montane rainforests in central Africa (Plumbtre *et al*., 2002). Nyungwe extends over an area of 1,019 km2 and covers an altitudinal range of 1,600 - 2950 m. In conjunction with the contiguous forest in Kibira National Park (400 km^2), Burundi, this forest is the largest block of lower montane forest in Africa (Weber, 1989; Vedder *et al*., 1992). The combination of large area of montane forest, a steep elevation gradient (ranging from 1600 to 2950 masl), and the high occurrence of endemism makes Nyungwe National Park a high priority area for conservation in Rwanda and within the Albertine Rift.

Meteorological data have been collected from within the forest by researchers at Uwinka from 1996 to present. Daily rainfall observations show that Nyungwe is characterized by an 8.5 month pluvial season starting in September that transitions rather abruptly to a dry season starting in mid-May that is punctuated by intermittent rainfall March shows the peak of the rainfall with rates of 8mm/day sustained for much of the month. At Uwinka the data offers no evidence for a short dry season around January, as has been occasionally reported. (Sun *et al*., 1996, Seimon & Picton Phillips, 2010). Temperatures at Nyungwe are cool with an average minimum temperature of 10.9° C and an average maximum temperature of 19.6° C (Sun *et al*., 1996). Analyses of phenological patterns of fruiting and flowering at Nyungwe show that fruit production peaks between March and May, leaf flush peaks in July and August, and flower production peaks in December and January (Sun *et al*., 1996, Chao *et al*., 2012).

The Nyungwe Forest hosts 319 species of bird, of which 26 are Albertine Rift endemics and 11 are classified as either Endangered, Vulnerable or Near Threatened (Chao, 2008; unpublished data; Plumptre *et al*., 2007). It is home to an abundant variety of plant life, including 47 locally endemic species of flowering plants and about 280 Albertine Rift endemics (Fischer & Killmann, 2008) and more than 260 species of trees and shrubs (Dowsett, 1990). A mammal list for Nyungwe shows 87 species, mostly rodents and bats, 14 endemics with 16 species classified as either Critically endangered, Endangered, Vulnerable or Near Threatened (unpublished data: Plumptre *et al*., 2007; IUCN, 2008). Of special significance is the high diversity of primates, including 13 different species, and representing 20% of all African primates. These include the endangered Eastern chimpanzee (*Pan troglodytes schweinfurthii*), the Owl-faced monkey (*Cercopithecus hamlyni),* l'Hoest's monkey (*Cercopithecus hoesti*) and the Angolan black and white colobus monkeys (*Colobus angolensis ruwenzorii*), living in groups of more than 300 individuals

WCS has been engaged in the conservation of Nyungwe since the mid-1980s, starting the '*Project de Conservation de la Foret de Nyungwe*' (PCFN) in 1984 (Plumbtre *et al*., 2002). The history of WCS-sponsored research and monitoring at Nyungwe is long and complex (Table 1). It involved initiatives including surveys (Vedder, 1988, Dowsett, 1990, Plumptre *et al*., 2002, in prep.) and research by various academics and conservationists on primates (Kaplan, 2001; Kaplan *et al*., 1998; Fashing *et al*., 2007), small mammals (Kerbis & Ntare, 2009), birds (Sun & Moermond, 1997; Sun *et al*., 1997), and tree phenologies (Sun *et al*., 1996; Plumbtre *et al*., 2012). Through time, research and monitoring programs have grown organically as new research projects were added to old ones, old research projects morphed into monitoring programs and long term monitoring was adjusted to budget priorities. Objectives have changed over time and new questions are being asked of old data and sampling that was designed for (now) outdated objectives. Meanwhile, data collection has continued unabated since 1995/6 with only cursory examination of the data being collected.

This report examines the trends in bird point count data and mammal line transect data collected over a period of 15 years, representing one of the largest, continuous datasets available for monitoring wildlife populations in an African tropical montane forest. Three major questions of interest concerning the Nyungwe monitoring data are: 1) what are the long term trends in mammal and bird populations over time; 2) how do trends in wildlife populations relate to conservation efforts over time; and 3) how do trends in wildlife populations relate to climate change. We assess question 2 using mammal data since hunting of mammals is likely to be most sensitive to interventions and patrolling by park guards. We assess question 3 with bird data since birds are more likely to respond to climate change by shifting altitudinal distribution and abundance in response to shifting rainfall and temperature.

STUDY AREA and SAMPLING DESIGN

The survey area lies in the central part of NNP, accessible by an unpaved highway (Figure 1). Although data collection resumed in 1996, we considered 1997 as the first year of data collection because there were a number of questions about the accuracy of surveys in 1996 (F. Maisel, in litt.). Between 1997 and 2011, 20 transects were established; in 1997, 10 transects were surveyed ($\bar{X}$ = 2.54 km, range 1.3 - 4.5 km), in 2003, 3 transects were added ($\bar{X}$ = 2.50 km, range 1.4 - 3.1 km), and in 2005, 7 more transects were added, all 2 km in length. Bird and mammal data were collected at the same time on the same survey. In 1997, transects were established in the Uwinka

(7 transects) and Gisakura (3 transects) study areas (Chao *et al*., 2012: Table 2) with an emphasis on transect location was to cover the altitudinal gradient in areas with easy access or near base

Table 1. History of research and monitoring at Nyungwe National Park, Rwanda

Year	Project
1984	WCS establishes Projet Conservation de la Forêt Nyungwe (PCFN)
1987	Vedder begins project on Angolan black and white colobus
1988	Vedder (1988) Final report with recommendations for training, monitoring and research
early 1990's	Kaplan starts work on l'hoesti's monkey and blue monkeys, tree phenology
early 1990's	Sun works on turacos and tree phenology
1994	Genocide disprupts research and monitoring, data lost
1995	PCFN monitoring re-established
1996	PCFN sets up tree phenology, mammal survey, bird survey
1996	PCFN sets up climate monitoring program
1996	Post-fire forest regeneration monitoring
1999	Parkwide biodiversity survey
1999	Seriostachys scandens monitoring
2000	Chimpanzee ecology, monitoring and habituation
2000	Grey-cheeked mangabey tracking
2003	Initiate ranger-based monitoring (MIST)
2006	Owl-faced monkey survey
2009	Parkwide biodiversity survey
2009	Chao summarizes bird and mammal monitoring data
2011	WCS data synthesis begins

camps. In 2003, transects were added in Cyamudongo forest fragment to evaluate the value of the area for bird tourism to complement ongoing chimpanzee-based tourism. In 2005, transects were added at Busoro, Uwasenkoko and Gasare study areas to increase coverage at lower elevations.

Habitat in Uwinka-Gisakura study area is primarily less disturbed forest, characterized by large fruit trees, closed canopy and intermittent gaps. Dominant species are *Sysygium guinense, Newtonia buchananii*, and *Entandrophragma exelsa*. Elevation ranges from 1800 - 2950 masl. Cyamudongo Forest is isolated forest fragment of approximately 4 km^2 and ranging in elevation from 1500 - 2100 masl. It is rich in primates, including chimpanzees, and was added to the park in 2004. The forest is located in primarily subsistence agriculture zone, surrounded by perennial crops of bean, cassava, corn, sweet potatoes, rice, sorghum, bananas, and various vegetable. Vegetation is dominated by tall tree closed and open canopy forest on steep slopes. Busoro study area is less disturbed forest dominated by tall trees under closed canopy and some open canopy. Elevation ranges from 1800 - 2180 masl. Uwasenkoko and Gasare site are similar in terms of habitat and range in elevation from 2250 - 2490 masl. These two sites have savanna and swamp vegetation. The area surrounding these sites has been much affected by bush fire in last 15 years.

Table 2. Distribution of transects and points, elevation range of transects, and time interval of data collection among study areas and sites. Uwinka and Gisakura study areas were not sampled in 2007.

Site	Transect	Length (km)	# points	Elev range (m)	Data Collection
Uwinka	Uwinka 1	1.3	14	2240-2410	1997 - 2011
Uwinka	Uwinka 2	2	21	2200-2520	1997 - 2011
Uwinka	Uwinka 3	2	21	2100-2460	1997 - 2011
Uwinka	Uwinka 4	2	21	2000-2460	1997 - 2011
Uwinka	Uwinka	3.1	32	2070-2460	1997 - 2011
Uwinka	Bururi	4.5	46	1830-2470	1997 - 2011
Uwinka	Bigugo	4.5	46	2380-2940	1997 - 2011
Gisakura	P. Chute	2	21	1767-1848	1997 - 2011
Gisakura	Karamba 1	2	21	1848-1917	1997 - 2011
Gisakura	Karamba 2	2	21	1870-1964	1997 - 2011
Cyamudongo	Cyamudongo A	3	31	1910-2140	2003 - 2011
Cyamudongo	Cyamudongo B	3.1	32	1820-2140	2003 - 2011
Cyamudongo	Cyamudongo C	1.4	12	1760-2070	2003 - 2011
Busoro	Busoro A	2	21	1800-2180	2005 - 2011
Busoro	Busoro B	2	21	1840-2150	2005 - 2011
Busoro	Busoro C	2	21	1840-2180	2005 - 2011
Gasare	Gasare A	2	21	2330-2340	2005 - 2011
Gasare	Gasare B	2	21	2250-2330	2005 - 2011
Uwasenkoko	Uwasenkoko A	2	21	2380-2490	2005 - 2011
Uwasenkoko	Uwasenkoko B	2	21	2360-2420	2005 - 2011

Intensity of poaching varies across the study areas. Poaching at Uwinka is believed to be relatively low because activities of research, tourism and anti-poaching have been concentrated here since 1989. Gisakura may have been affected by poaching activities before 2003 when a permanent anti-poaching team was deployed in this site. Cyamudongo presumably has a high level of poaching due to its isolated status and small size. The remaining sites have relatively high levels of poaching and Busoro has mining activity nearby.

Sampling effort was unequal over time and over elevation (Table 3, Figure 2). Efforts ranged from 12 months across 10 transects (305 km of line transects and 2,424 point counts) in 1997, to 1 month across 20 transects (47 km of line transects and 385 point counts) in 2009, to 20 transects across 2 months (141 km of line transects and 773 point counts) in 2010 and 2011. In 2012 no monitoring was conducted. Much of the variation in sampling effort was due to budget constraints (most years), a park-wide survey in 1999 and 2009 (Plumptre *et al*. 2002; Chao *et al*., 2010) and a temporary decision to halt monitoring in 2007 (A. Plumptre, pers. comm.). All transects start from a road or base camp and are oriented into the park. Transects range from 1,600 to 2,950 m in elevation, and represent the entire range of elevation for the park. At 100 m intervals, the habitat has been characterized, elevation noted, trees in fruit and flower are noted monthly.

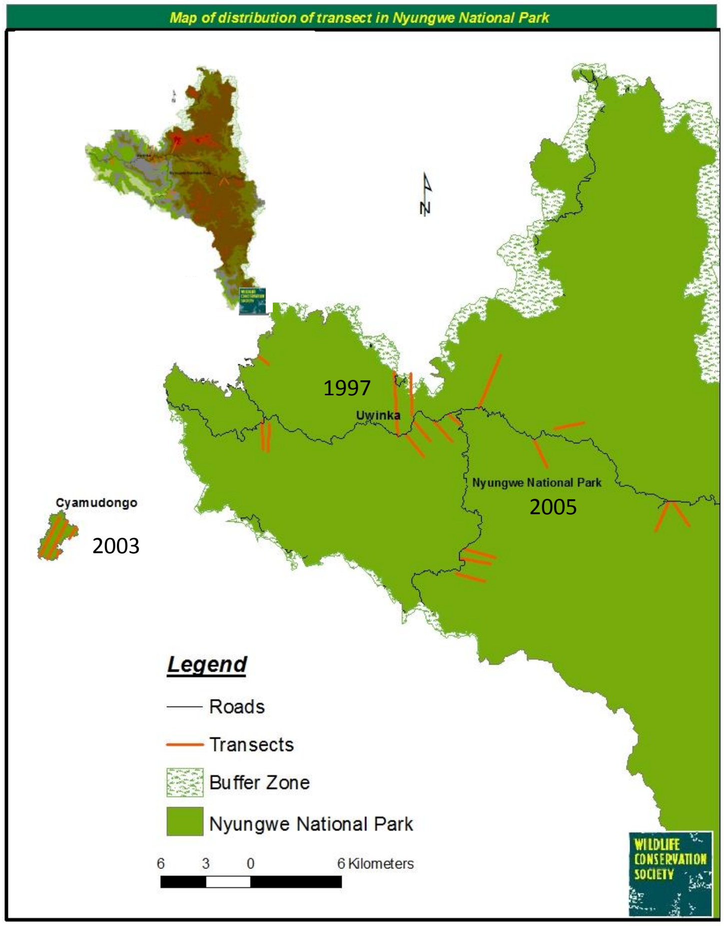


Figure 1. Location of survey transects and year of establishment.

One result of the unequal sampling effort is that over time, the distribution of sampling shifted downward over time to middle and lower elevations (Figure 2), increasing the likelihood of encountering lower elevation species (e.g. Mona monkeys). This can affect density estimates made under the assumption that detection probability remains constant over time, an assumption that is often necessary when making multi-year density estimates using sparse data.

Table 3. Distribution of sampling effort (# months of sampling/# points sampled) over time on eaach point transect In Nyungwe NP.

Site	Transect	Length (km)	# points	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Uwinka	Uwinka 1	1.3	14	12/168	12/168	5/70	3/42	3/42	4/56	4/56	6/84	4/56	3/42	0/0	1/14	1/14	2/28	2/28
Uwinka	Uwinka 2	2	21	12/252	12/252	5/105	3/63	3/63	4/84	4/84	6/126	4/84	3/63	0/0	1/21	1/21	2/42	2/42
Uwinka	Uwinka 3	2	21	12/252	12/252	5/105	3/63	3/63	4/84	4/84	6/126	4/84	3/63	0/0	1/21	1/21	2/42	2/42
Uwinka	Uwinka 4	2	21	12/252	12/252	5/105	3/63	3/63	4/84	4/84	6/126	4/84	3/63	0/0	1/21	1/21	2/42	2/42
Uwinka	Uwinka	3.1	32	12/192	12/192	5/80	3/47	3/48	4/64	4/64	6/65	4/64	3/48	0/0	1/16	1/16	2/32	2/32
Uwinka	Bururi	4.5	46	12/276	12/274	5/114	3/69	3/69	4/92	4/92	6/91	4/92	3/69	0/0	1/23	1/23	2/46	2/46
Uwinka	Bigugo	4.5	46	12/276	12/276	5/115	3/71	3/69	4/91	4/92	6/92	4/92	3/69	0/0	1/23	1/23	2/46	2/46
Gisakura	P. Chute	2	21	12/252	12/252	5/105	3/63	3/63	4/84	4/84	6/126	4/84	3/63	0/0	1/21	1/21	2/42	2/42
Gisakura	Karamba 1	2	21	12/252	12/252	5/105	3/63	3/63	4/84	4/84	6/126	4/84	3/63	0/0	1/21	1/21	2/42	2/42
Gisakura	Karamba 2	2	21	12/252	12/252	5/105	3/63	3/63	4/84	4/84	6/126	4/84	3/63	0/0	1/21	1/21	2/42	2/42
Cyamudongo	Cyamudongo A	3	31	0/0	0/0	0/0	0/0	0/0	0/0	1/16	3/47	4/62	3/46	3/46	3/47	1/15	2/31	2/31
Cyamudongo	Cyamudongo B	3.1	32	0/0	0/0	0/0	0/0	0/0	0/0	1/16	2/32	4/64	3/48	3/48	3/48	1/15	2/32	2/32
Cyamudongo	Cyamudongo C	1.4	12	0/0	0/0	0/0	0/0	0/0	0/0	1/6	3/18	4/24	3/18	3/18	2/12	1/6	2/12	2/12
Busoro	Busoro A	2	21	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	3/63	3/63	3/63	3/63	1/21	2/42	2/42
Busoro	Busoro B	2	21	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	3/63	3/63	3/63	3/63	1/21	2/42	2/42
Busoro	Busoro C	2	21	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	3/63	3/63	3/63	3/63	1/21	2/42	2/42
Gasare	Gasare A	2	21	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2/42	3/63	3/63	3/63	1/21	2/42	2/42
Gasare	Gasare B	2	21	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2/42	3/63	3/63	3/63	1/21	2/42	2/42
Uwasenkoko	Uwasenkoko A	2	21	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2/42	3/63	3/63	3/63	1/21	2/42	2/42
Uwasenkoko	Uwasenkoko B	2	21	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2/42	3/63	3/63	3/63	1/21	2/42	2/42

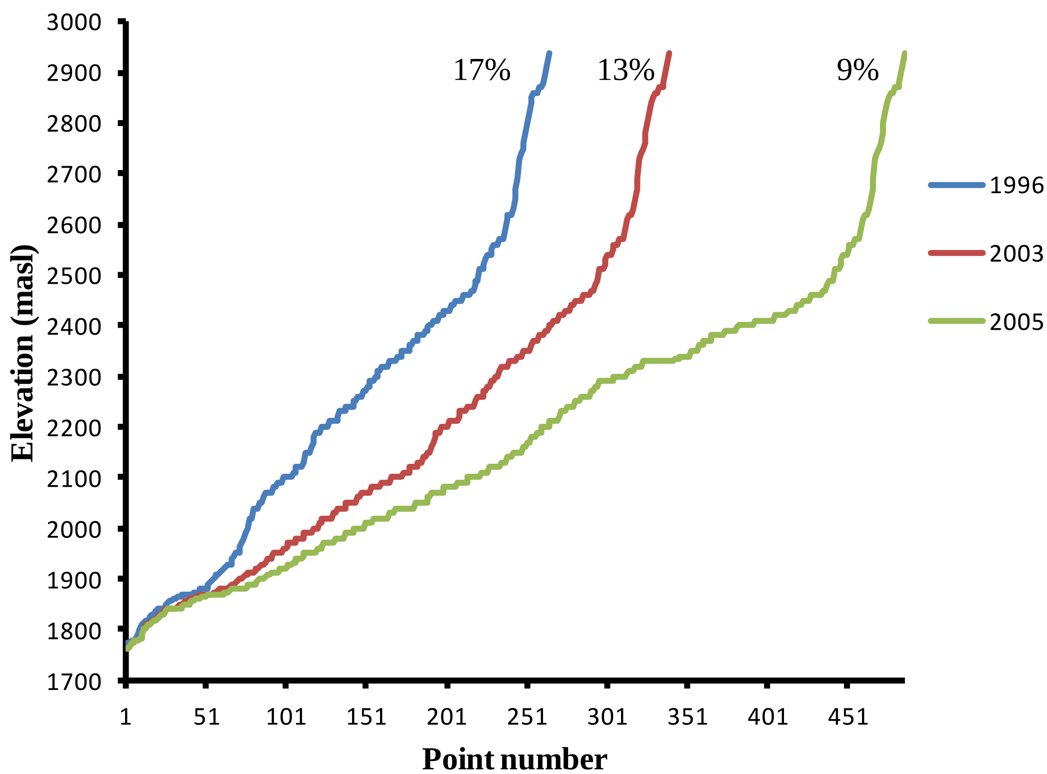


Figure 2. Expansion of sampling effort (x-axis) and altitudinal distribution of points (y-axis) along transects for 1996 (10 transects), 2003 (13 transects) and 2005 (20 transects). Number to left of each line indicates the percentage of points above 2,500 masl.

NYUNGWE NATIONAL PARK MAMMALS

Mammals have been a topic of interest in Nyungwe National Park since the late 1980's. The park mammal list features 98 mammal species, excluding species known to be extinct. It has 12 primate species including chimpanzee (*Pan troglodytes*) and the Owl-faced monkey (*Cercopithecus hamlyni*) and super-groups of Angolan black and white colobus (*Colobus angolensis*) numbering more than 300 individuals. There are also 14 carnivore species recorded from the park, though several species have not been seen since in the past decade. Recent camera trap surveys have added a new mammal to the Nyungwe species list, the honey badger or ratel (*Mellivora capensis*). Two-thirds of the mammal list is composed of small mammals, including rodents, insectivores and bats, and the remaining one-third are considered large mammals (Table 4).

Mammal populations in NNP have been under pressure from human exploitation for a long time and several species are now extinct or nearly extinct within the park (Table 4). The general pattern of decline in mammal encounter rates strongly suggests a common agent, most likely poaching. The pattern of species loss is typical of feeding down the food chain with loss of buffalo in the1970's, giant forest hog in the 1980's (3rd largest mammal), and elephant in 1999. By the late 1980's, bush pig, bushbuck, and three duiker species were already rare (4th, 5th, 6th, 11th, 12th largest mammals), and encounter rates of large squirrels and large rodents today (70 g Boehm'a squirrel and larger) were declining. It is also possible that declines in encounter rates of many primates may also linked to hunting due to a breakdown in local taboos about eating primates, bushmeat trade for cross-border markets in Burundi and Congo, and local demand for bushmeat by Chinese road builders. The recent extirpation of the mega-fauna may also be contributing to vegetation change. Blake *et al*., (2009) found that the loss of elephants and other large-bodied seed dispersers from forest habitats may lead to a wave of recruitment failure among animal-dispersed tree species, favouring the regeneration of abiotically dispersed guilds of trees. In Nyungwe forest, the total extirpation of elephants (*Loxodonta africana*) and forest buffalo (*Syncerus caffer nanus*), and the much reduced populations of duikers and bushbuck may therefore cause a cascade throughout the forest ecosystem, with some flora failing to recruit new cohorts. Over time, this may lead to the alteration of the forest structure and characteristics. Additionally, loss of forest browsers also may reduce seedling/sapling mortality, resulting in unpredictable changes in forest composition and structure (Augustine & McNaughton, 2004).

METHODS: Mammals

Mammal surveys were conducted From 1997 to 2011 (Table 3) along transects that range in length from 1.3 to 4.5 km, and are conducted at the same time as point count surveys for birds. Survey effort was variable over time and space. Typically, technicians work in 2-3 person teams with one recorder and two observers. Data are collected on direct (visual, aural) and indirect (sign) observations for primates, other arboreal mammals and terrestrial mammals. Each observation is located along the trail relative to marked bird count stations at 100m intervals. For example, an observation whose perpendicular distance intersects the trail at 35 m from the 300 point count station, would be labeled 335 m. The perpendicular distance from the trail to the mammal was measured for visual observations out to 70 m using a laser rangefinder. Beyond 70 m, all distances were estimated. Aural observations were estimated at all distances. Primate species are recorded as direct observations of groups and individuals, as well as nests for chimpanzees. Squirrel data consisted primarily of direct observations. Terrestrial mammals are recognized by a mix of sign and direct observation.

Table 4. Medium to large sized mammals of Nyungwe National Park, including body weight, IUCN status and status in park.

Family	Genus	Species	Common Name	Body size (kg)	IUCN Status	Status in NNP
Hominidae	Pan	troglodytes	Chimpanzee	35	EN	Uncommon
Cercopithecidae	Colobus	angolensis	Angolan colobus	15	LC	Uncommon
Cercopithecidae	Papio	anubis	Olive Baboon	35	LC	Uncommon
Cercopithecidae	Lophocebus	albigena	Grey-cheeked Mangabey	9	LC	Uncommon
Cercopithecidae	Cercopithecus	aethiops	Vervet monkey	7	LC	Uncommon
Cercopithecidae	Cercopithecus	lhoesti	L'hoest's monkey	8	VU	Common
Cercopithecidae	Cercopithecus	mona	Mona's monkey	5	LC	Uncommon
Cercopithecidae	Cercopithecus	hamlyni	Owl-faced monkey	8	VU	Rare
Cercopithecidae	Cercopithecus	ascanius	Redtail monkey	5	LC	Uncommon
Cercopithecidae	Cercopithecus	mitis	Blue monkey	7	LC	Common
Loridae	Perodicticus	potto	Bosman's potto	1.2	LC	Unknown
Galagonidae	Galago	senegalensis	Senegal galago	0.25	LC	Unknown
Sciuridae	Funisciurus	carruthersi	Carruther's Mountain Tree Squirrel	0.27	LC	Unknown
Sciuridae	Funisciurus	pyrropus	Cuvier's Fire-footed Squirrel	0.23	LC	Unknown
Sciuridae	Paraxerus	alexandri	Alexander's squirrel	0.06	LC	Unknown
Sciuridae	Paraxerus	boehmi	Boehm's squirrel	0.07	LC	Unknown
Sciuridae	Heliosciurus	ruwenzorii	Montane Sun Squirrel	0.29	LC	Unknown
Sciuridae	Protoxerus	stangeri	African Giant Squirrel	0.77	LC	Unknown
Hystricidae	Atherurus	africanus	Brush-tailed porcupine	2.75	LC	Common
Thryonomyidae	Thryonomys	gregorianus	Marsh Cane Rat	6.5	LC	Unknown
Cricetidae	Otomys	denti	Montane Groove-toothed Rat	0.13	LC	Unknown
Cricetidae	Otomys	tropicalis	Tropical Groove-toothed Rat	0.13	LC	Unknown
Cricetidae	Cricetomys	gambianus	Forest Pouched Rat	1.2	LC	Unknown
Canidae	Canis	adustus	Side-striped Jackal	9.5	LC	Rare
Mustelidae	Melivora	capensis	ratel	11.5	LC	Rare
Lutrinae	Aonyx	congicus	Congo Clawless Otter	23	LC	Rare
Herpestidae	Herpestes	ichneumon	Ichneumon Mongoose	3.2	LC	Unknown
Herpestidae	Herpestes	sanguineus	Slender mongoose	0.55	LC	Unknown
Herpestidae	Atilax	paludinosus	Marsh Mongoose	3.6	LC	Unknown
Viverridae	Genetta	tigrina	Blotched Genet	2.2	LC	Unknown
Viverridae	Genetta	servalina	Servaline Genet	1.5	LC	Unknown
Viverridae	Civettictis	civetta	African Civet	13.5	LC	Unknown
Viverridae	Nandinia	binotata	African Palm Civet	1.6	LC	Unknown
Felidae	Felis	silvestris	Wild Cat	4.7	LC	Unknown
Felidae	Felis	Serval	Serval	12	LC	Rare
Felidae	Felis	aurata	Golden Cat	12	NT	Extinct?
Felidae	Panthera	pardus	Leopard	50	NT	Extinct
Manidae	Manis	tricuspis	African white-bellied pangolin	2.3	NT	Unknown
Procaviidae	Dendrohyrax	dorsalis	Western Tree Hyrax	3	LC	Common
Elephantidae	Loxodontra	africanus	African elephant	3000	EN	Extinct
Suidae	Potamochoerus	larvatus	Bushpig	100	LC	Rare
Suidae	Hylochoerus	meinertzhageni	Giant Forest Hog	200	LC	Extinct
Bovidae	Syncerus	caffer	African Buffalo	550	LC	Extinct
Bovidae	Tragelaphus	scriptus	Bushbuck	55	LC	Rare
Bovidae	Cephalophus	nigrifrons	Black-fronted duiker	16	LC	Uncommon
Bovidae	Cephalophus	silvicultor	Yellow-backed duiker	62	LC	Rare
Bovidae	Cephalophus	weynsi	Weyn's duiker	15	LC	Unknown

Distribution Analysis

We estimated the distribution (proportion of study area occupied) and density (individuals/km^2) of each species for which there were sufficient data (Table 5). Brush-tailed porcupine (*Atherurus africanus*), Giant pouched rat (*Cricetomys gambianus*), Bushpig (*Potamochoerus larvatus*) Black-fronted duiker (*Cephalus nigrifrons*), and Yellow-backed duiker (*Cephalus silvicultor*) were detected primarily by sign and we did not attempt to estimate density for these species. We also did not attempt to estimate density for the Angolan colobus (*Colobus angolensis*) because they occur in super-groups and estimates of group size were not reliable.

We used multi-season occupancy models in PRESENCE 5.5 (MacKenzie *et al*., 2006) to estimates the proportion of the study area occupied by each species. In an occupancy analysis, a particular sampling unit can be in one of three states in respect to presence or absence of a species: occupied and species detected, occupied but species not detected, and not occupied. We use replicated sampling to develop detection histories for each sample unit, and the patterns of detection histories are used to estimate the probability that a site is occupied. The replications can be over time, by different survey teams, or spatial. Figure 3 illustrates the sampling strategy based on Pollock's Robust Design (Pollock, 1982).

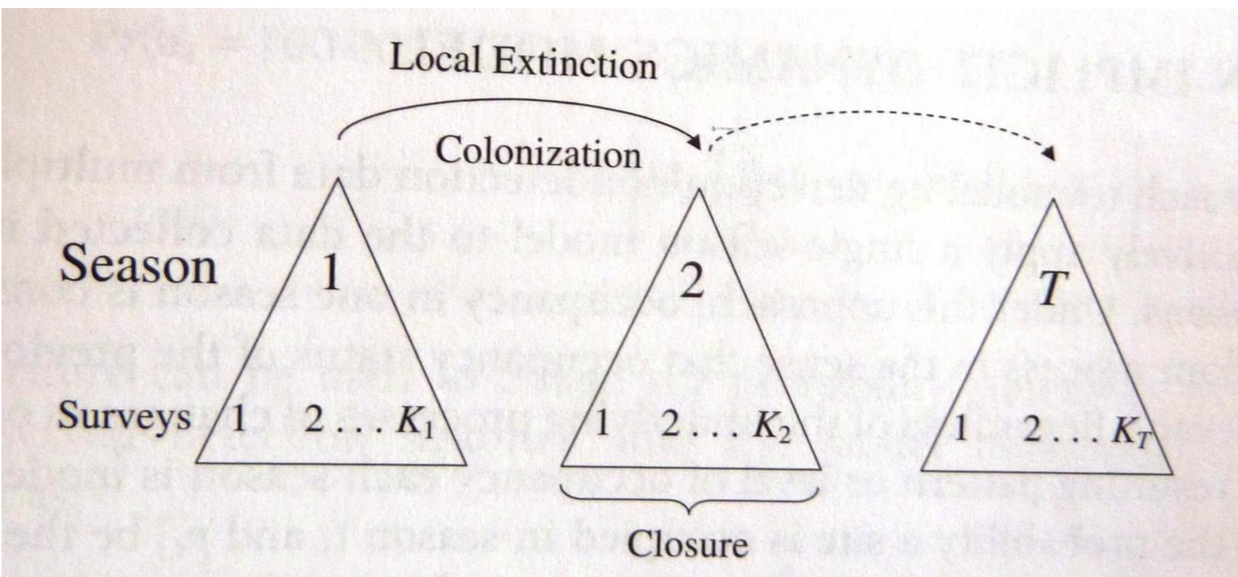


Figure 3. Graphical representation of the situation for a multi-season occupancy study. Each triangle represents a season (t), with multiple (K) surveys within season. Sites are closed to changes within seasons, but changes may occur between seasons through the process of local colonization and local extinction.

To adapt the line transect surveys to an occupancy analysis, we first split each transect into 100 m segments and treated 5 consecutive segments as replications for a 500 m sampling unit. For transects that had a leftover segment less than 500 m long, we assumed that the shortfall was a missing value. A 300 m sampling unit for example would have 3 replicates and 2 missing values.

This approach resulted in 95 sampling units per year. Because of the high variability in sampling effort each year (1 to 12 months) we combined all observations each year, and treated the months of sampling effort as a covariate that might affect annual detection probabilities. We also treated

Table 5. Species detected on line transect surveys, number of observations (* indicates inclusion in occupancy analysis, ** indicates inclusion in occupancy and density analysis), and strata of activity. Duikers were analyzed as a group.

Species	Common name	Frequency	Habit
Galago senegalensis	Eastern Needle-clawed Galago	1	Arboreal
Cercopithecus lhoesti	L'hoest's monkey	232**	Semi-terrestrial
Cercopithecus mitis	Blue monkey	667**	Semi-terrestrial
Cercopithecus ascanius	Redtail monkey	4	Arboreal
Cercopithecus mona	Mona's monkey	65**	Arboreal
Colobus angolensis	Angolan colobus	62**	Arboreal
Lophocebus albigena	Grey-cheeked Mangabey	260**	Arboreal
Papio anubis	Baboon	31	Terrestrial
Pan troglodytes	Chimpanzee	417**	Semi-terrestrial
Heliosciurus ruwenzorii	Montane Sun Squirrel	369**	Arboreal
Ecureil ruwenzori	Ruwenzori squirrel	5	Arboreal
Funisciurus pyrropus	Cuvier's Fire-footed Squirrel	130**	Arboreal
Paraxerus boehmi	Boehm's squirrel	421**	Arboreal
Protoxerus stangeri	African Giant Squirrel	13	Arboreal
Anomalurus derbianus	Lord Derby's Anomalure	25	Arboreal
Atherurus africanus	Brush-tailed porcupine	111*	Terrestrial
Otomys denti	Groove-toothed Rat	6	Terrestrial
Cricetomys gambianus	Cricetomys gambianus	137*	Terrestrial
Canis adustus	Side-striped Jackal	3	Terrestrial
Ictonyx striatus	Zorilla	1	Terrestrial
Genetta servalina	servaline genet	1	Semi-terrestrial
Felis serval	Serval	6	Terrestrial
Dendrohyrax dorsalis	Tree Hyrax	7	Arboreal
Potamochoerus larvatus	Bushpig	160*	Terrestrial
Cephalophus nigrifrons	Black-backed duiker	49*	Terrestrial
Cephalophus silvicultor	Yellow-backed duiker	3*	Terrestrial
Cephalophus sp.	Unknown Duiker	2*	Terrestrial

elevation of observation, and forest cover type (closed forest, open forest, other habitat) as covariates that might affect mammal occupancy. Each year was considered a primary sampling unit and population closure was assumed within years.

There are several features and assumptions of the sampling scheme that require clarification. First, because of small sample sizes, we combined all data for a year into annual surveys.

Transects that were added later in the study are assumed to have missing values in the early years. We have assumed that the sample sites have been chosen from an area of interest with the intent to establish the presence or absence of a species. The choice of sampling units should be representative of the area of interest if we wish to make valid inferences. In this project, logistical constraints required that transects were placed close to access points and close to infrastructure (camps) and cannot be considered a random sample of the entire park. However, comparisons within the study area over time should be valid. We also have 4 assumptions associated with occupancy analysis: (1) occupancy status at each site does not change over the survey season (population closure); (2) the probability of occupancy is constant across sites and any differences are modeled using covariates; (3) the probability of detection is constant across all sites and surveys or is a function of site-survey covariates; and (4) detection of species and detection histories at each location are independent. If these assumptions are not met, estimates may be biased leading to incorrect inferences.

If species randomly move in and out of a sampling unit, the estimates should be unbiased but the inference is more closely related to use of sampling units than occupancy of the units. If a species makes non-random moves into or out of the area, then the resulting estimates will be biased. The impact of unmodeled heterogeneity in occupancy probabilities is unknown though it is suspected that the average occupancy values will be relatively unbiased but the variance may be larger than expected. Heterogeneity in detection probability will often result in negatively biased estimates and as the size of the study decreases (few sites, few replications) bias is exaggerated. If detection is not independent among sites, the precision of the occupancy estimate is usually overstated. Nonindependence often arise when sampling sites are too close together, or replications are too close such that an initial detection increases the likelihood of subsequent detection (spatial autocorrelation).

In this monitoring design, we may have some violations of assumptions due to the use of consecutive spatial replicates within a sampling unit. However, at the time of analysis, there are no options in occupancy analysis for multi-season spatial autocorrelation models, and any biases incurred should be consistent over time within sampling units, making comparisons valid within the survey, although we should extrapolate with care.

We used the multi-season occupancy models to examine the trends in distribution for species over time, and also to test whether there were elevation effects in distribution and whether there were habitat differences in distribution. Multi-season occupancy models include several approaches to parameterization. If we define probability of occupancy as ψ, detection probability as p, local colonization as γ and local extinction as ε, then the modeling approaches can be described as:

1. ψ, $\gamma(t)$, $\varepsilon(t)$, $p(t)$ in which we estimate initial occupancy, seasonal colonization and extinction and seasonal detection probability. Subsequent seasonal occupancy values are calculated as a function of γ and ε.
2. $\psi(t)$, $\gamma(t)$, $p(t)$ in which we estimate seasonal occupancy, colonization and detection, and local extinction is a combination of $\psi(t)$ and $\gamma(t)$.
3. $\psi(t)$, $\varepsilon(t)$, $p(t)$ in which we estimate seasonal occupancy, extinction and detection, and local colonization is a combination of $\psi(t)$ and $\varepsilon(t)$.
4. ψ, $\gamma(t)$, $\varepsilon(t)$, $p(t)$ where $\varepsilon(t) = 1 - \gamma(t)$.

We incorporated two covariates in initial models; number of months of sampling as a covariate of detection probability and elevation as a covariate of occupancy. We chose the most parsimonious model based on minimum AIC criteria (Burnham and Anderson 2002). If there was strong support for more than one model, we chose the top model and did not attempt to use model averaging.

Density analysis

We analyzed temporal patterns of density for primates and squirrels (Table 5) using distance-based sampling and Distance 6.0 Software (Thomas *et al*., 2010). Distance software uses the distribution of perpendicular distances from the transect to the animal(s) to estimate the probability of observing an animal or group of animals at a given distance from the transect (Buckland *et al*., 2010). From this probability distribution, we can deduce the effective strip width for the survey (the distance at which the number of individuals missed at shorter distances is equal to the number of individuals observe at greater distances) and estimate the density of animals observed during the survey (Thomas *et al*., 2010). As in the occupancy analysis, we have a set of assumptions that must be satisfied for the result to be unbiased: (1) Animals on the transect line are observed with certainty (detection = 100%); (2) Objects do not move and distances are calculated from the point of initial detection if they do move; (3) Measurements are exact; (4) animal locations are independent of the positions of the transects; and (5) detections are independent events. Buckland *et al*. (2010) discuss the ramifications of failure to meet these assumptions and ways to overcome logistical difficulties in designing distance surveys for forest primates.

Modeling of distance data for density estimation requires fitting a number of different distributions to find one that fits the observed data reasonably well. Well-behaved data tend to be monotonically decreasing (observations decline with increasing distance), high detection close to the transect, a broad detection shoulder close to zero, and a sufficient number of observations (minimum 30). We evaluated three sets of models for each species: (1) a Half-normal model with cosine and Hermite polynomial adjustment terms; (2) a Hazard model with cosine and Hermite polynomial adjustment terms; and a Uniform distribution model with cosine and Hermite polynomial adjustment terms. The half normal distribution is, as it sounds half of a normal distribution, truncated at zero. The hazard function is used in survival analysis and can be developed to have a nice shoulder using adjustment terms. The uniform distribution has a constant detection probability at all distances, but can be molded to a monotonic declining function using the adjustment terms. All analyses treat the data as annual, varying effort is incorporated as number of km walked per transect (a 2 km transect walked for 12 months received 24 km effort). Because of small sample sizes (average of 4 to 44 observations/species/year), we estimated one detection probability for the entire study, assuming that detection was constant over time, and post-stratified the analysis by year to generate annual density estimates for each species. We determined the most parsimonious model is determined using minimum AIC criteria.

In distance analysis, the density estimate and the variance are affected by three estimated parameters; the encounter rate, the group size, and the detection probability. We estimate the encounter rate as the number of encounters per kilometer of transect walked and the group size as either the arithmetic mean, or some distance-corrected mean value. The detection probability is estimated by modeling described above. When a constant detection probability over time is assumed, the variation in density over time is reduced to a function of encounter rate and group size. In Nyungwe NP, as the survey was expanded and more low elevation transects were added, changes in encounter rate and group size may occur that affect the density estimates. These changes in density reflect changes in sampling design, temporal change or some combination of both and cannot be disentangled at this time. Where appropriate, we present results of the entire time series, and also break the results at 2004 to reflect the original 10 transect data set, and then the addition of 10 more transects.

RESULTS: Mammals

Primates Distribution and Abundance

We present results by species group. For occupancy results, we present the top three models, discuss the significance of covariates, and present the trend in distribution over time. For density estimates, we present the results in table and graphic form. We recorded 26 mammal species on the line transect surveys between 1997 and 2011. Ten species had less than 10 observations over the entire survey period and 3 species 31 or less observations; we did not attempt to analyze trends for these species. Of the remaining species, we made density estimates for primates and squirrels, and we made occupancy estimates for all remaining species.

Table 6. Summary of occupancy results and trends for primates, squirrels and terrestrial mammals. The trend is the slope of the linear regression over time and represents average annual change in proportion of study area occupied.

PRIMATES	Common Name	N	Occupancy		Detection		Trend
			min	max	min	max	
P. troglodytes	Chimpanzee	667	0.4615	0.8664	0.0778	0.2129	-0.0181
C. mitis	Blue Monkey	417	0.6941	0.9571	0.0742	0.1603	-0.0259
C. l'hoesti	L'Hoest's Monkey	232	0.484	0.8065	0.0477	0.0976	-0.0212
C. mona	Mona Monkey	65	0.2318	0.3497	0.0481	0.0481	-0.0084
L. albigena	Grey-cheeked Mangabey	260	0.3527	0.7363	0.0703	0.1471	-0.0194
C. angolensis	Angolan Colobus	62	0.2244	0.4195	0.0174	0.0645	0.01
SQUIRRELS							
P. boehmi	Boehm's Squirrel	421	0.5114	0.6621	0.0663	0.1685	-0.0103
H. ruwenzorii	Montane Sun Squirrel	369	0.441	0.9481	0.0555	0.1945	-0.028
F. pyrropus	Cuvier's fire-footed Squirrel	130	0.366	0.9364	0.0282	0.0748	-0.031
TERRESTRIAL MAMMALS							
C. sp.	Black-fronted/Yellow-backed duiker	54	0.052	0.169	0.1142	0.1142	-0.006
A. africanus	Bush-tailed porcupine	111	0.2081	0.2515	0.0194	0.0714	-0.0031
C. gambiensis	Giant pouched rat	137	0.1914	0.4657	0.0975	0.0975	-0.0178
P. larvatus	Bushpig	160	0.0438	0.239	0.1233	0.1233	0.0131

Between 1997 and 2011, primate populations contracted in distribution throughout the study area (Table 6) with the exception of Angolan colobus monkeys. Angolan colobus monkeys appear to have expanded their distribution during this time. Most decreases in primate distribution were steepest early in the monitoring period (1997 – 2001) and then became stable in later years.

Declines ranged from 27% in Chimpanzee distribution to 52% for Grey-cheeked mangabey. In contrast Angolan colobus increased their distribution by 87%, nearly doubling their distribution.

Table 7. Parsimonious model results for occupancy analysis results for primates.

Blue Monkey	AIC	ΔAIC	AIC wgt	no.Par.	Elevation	Effort
ψ,γ(),ε(),p(Effort)	3236.58	0	0.473	5		Sig. +
ψ,γ(),ε(Elevation),p(Effort)	3237.56	0.98	0.2898	6	NS -	Sig. +
ψ,γ(Elevation),ε(),p(Effort)	3237.96	1.38	0.2372	6	NS +	Sig. +
L'Hoestes monkey						
ψ,γ(),ε(),p(Effort)	1692.14	0	0.5853	5		Sig. +
ψ,γ(),ε(Elevation),p(Effort)	1692.83	0.69	0.4145	6	NS +	Sig. +
Mona Monkey						
ψ,γ(),ε(),p()	613.14	0	0.3846	4		
ψ,γ(),ε(),p(Effort)	613.15	0.01	0.3827	5		NS -
ψ(),γ(),p()	614.6	1.46	0.1854	3		
Angolan Colobus						
ψ,γ(Elevation),ε(Elevation),p(Effort)	631.84	0	1	7	NS +	Sig. +
Grey-cheeked Mangabey						
ψ,γ(),ε(Elevation),p(Effort)	1660.68	0	1	6	Sig. +	Sig. +
Chimpanzee						
ψ,γ(),ε(),p(Effort)	2354.98	0	0.6491	5		Sig. +
ψ,γ(),ε(Elevation),p(Effort)	2356.21	1.23	0.3509	6	NS +	Sig. +

Occupancy models that considered detection probability to be a function of effort performed consistently better than models that treated detection probability as constant (Table 7). As months of sampling increased, detection probability increased for every primate except the Mona monkey; the top two models had nearly equal weights (0.3846 versus 0.3827) between constant detection probability and effort-specific detection probability.

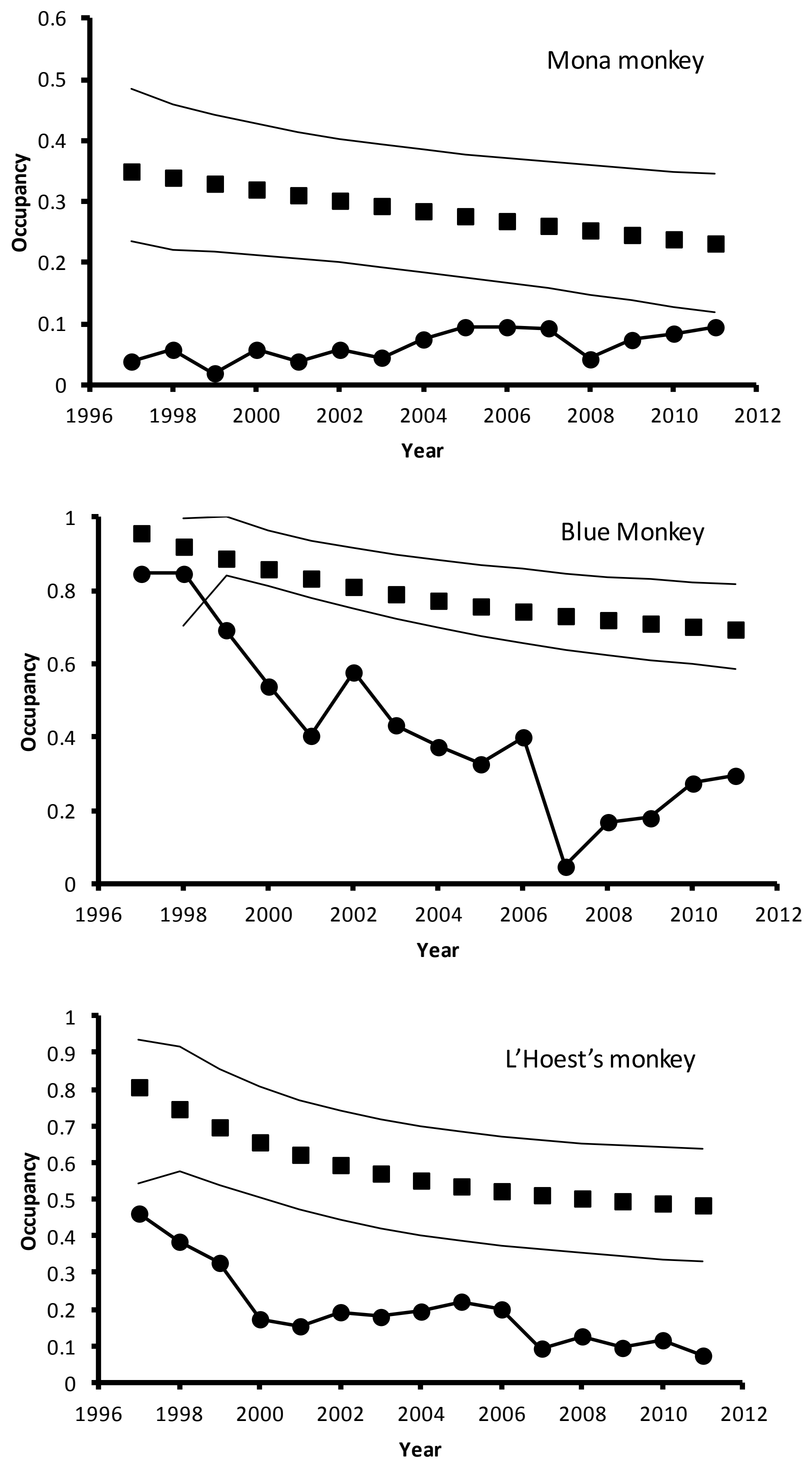


Figure 4. Observed (closed circle) and estimated occupancy (filled squares) for Mona, Blue and L'Hoest's monkeys. Estimated occupancy bounded by 95% confidence intervals.

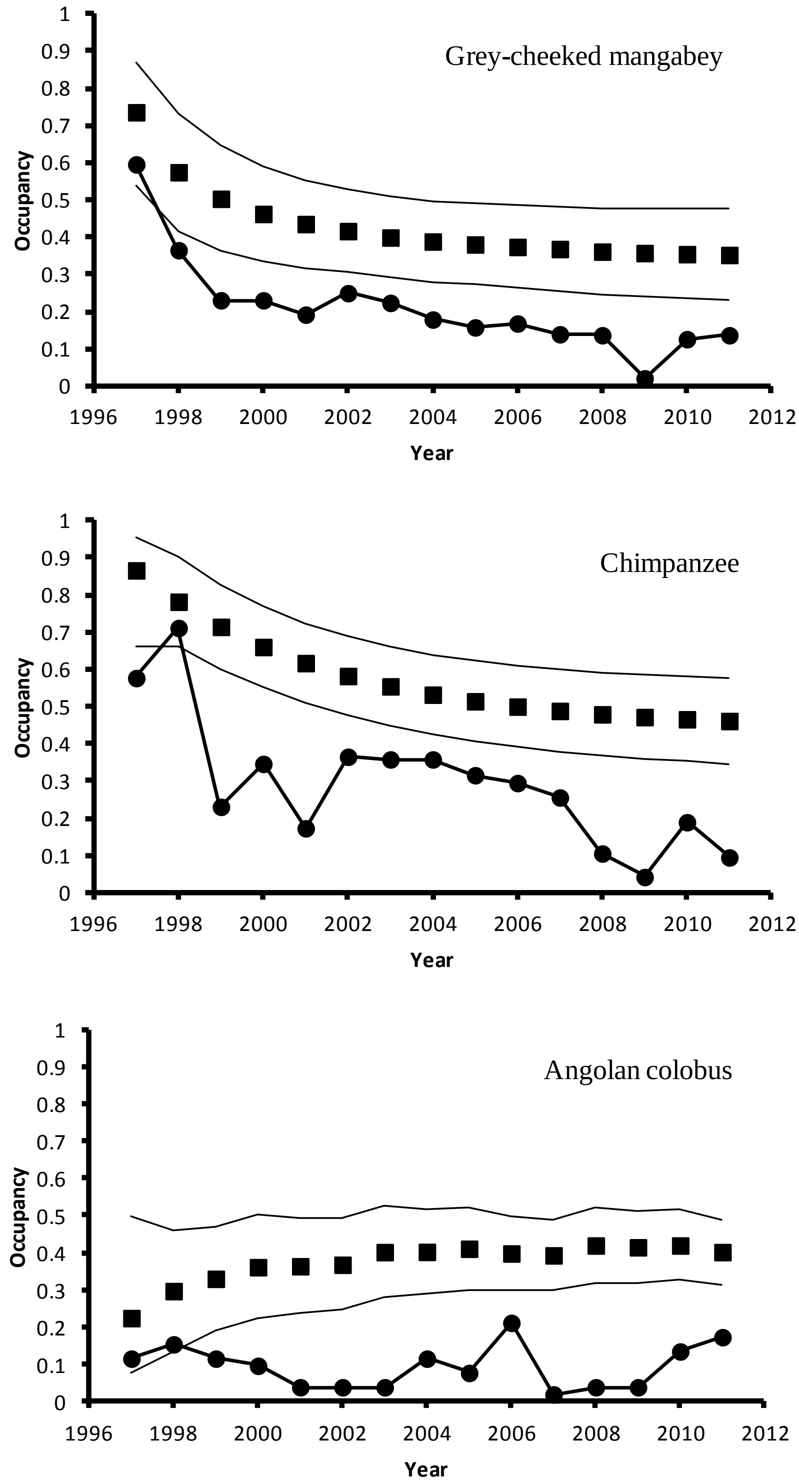


Figure 5. Observed (closed circle) and estimated occupancy (filled squares) for Grey-cheeked mangabey, Chimpanzee and Angolan colobus monkeys. Estimated occupancy bounded by 95% confidence intervals.

There was a general and consistent support for local extinction probability to be higher at higher elevation, meaning that occupancy tended to decline at higher elevations. This effect was significant only for Grey-cheeked mangabey. Table 6 shows the range of occupancy and detection probability for all species. Figure 4 shows the trends in distribution compared to the observed proportion of habitat occupied for Mona, Blue and L'Hoest's monkey, and Figure 5 shows the same for Grey-cheeked mangabeys, Chimpanzees and Angolan colobus monkeys. Estimated occupancy is significantly higher than the observed occupancy due to low probabilities of detection for all species in almost all years.

Densities of primates varied by species and over time (Table 8, Figure 6), primarily due to differences in group size and encounter rates. For example, Chimpanzee group size varied from 1.9 to 4.6, and encounter rates varied from 0.05/km of transect to 0.24/km of transect. Most of this variability reflects sampling error. Linear trends in density were generally not significant, except for Mona monkey and Grey-cheeked mangabey. Mona monkey showed a consistent increase in density over time, due to increasing in encounter rates. The decline in Grey-cheeked mangabey, apparently was due to a decline in encounter rates accompanied by a decline in group size.

Table 8. Results of line transect density estimates and trends (L = linear and Q = quadratic curve). L. trend is the slope of the linear regression (1997-2011) and Sig. refers to the significance level. Q. Trend is evaluated relative to linear trend and values with an asterisk (*) indicate that the quadratic fit was a marked improvement over the linear fit

PRIMATES	Common Name	N	Density		Group size		Encounter rate		P	L. Trend	Sig.	Q. Trend
			min	max	min	max	min	max				
P. troglodytes	Chimpanzee	284	0.191	1.03	1.92	4.62	0.047	0.237	0.864	-0.0045	NS	NS
C. mitis	Blue Monkey	613	0.64	7.35	1	3.88	0.167	0.805	0.432	0.027	NS	0.05*
C. l'hoesti	L'Hoest's Monkey	222	2.45	6.96	2.18	5.15	0.062	0.171	0.365	-0.128	NS	NS
C. mona	Mona Monkey	63	0	7.7	0	15	0	0.15	0.324	0.442	0.01	0.01
L. albigena	Grey-cheeked Mangabey	260	0.55	1.37	2.36	5.79	0.021	0.169	0.606	-0.0514	0.05	0.05
C. angolensis	Angolan Colobus	58	0	9.46	0	77	0	0.0856	0.658	0.253	NS	0.05*
SQUIRRELS												
P. boehmi	Boehm's Squirrel	387	3.04	7.48	1	1.37	0.126	0.26	0.428	-0.167	0.1	0.01*
H. ruwenzorii	Montane Sun Squirrel	216	0.96	5.47	1	1.33	0.056	0.264	0.571	-0.226	0.01	0.01*
F. pyrropus	Cuvier's fire-footed Squirrel	216	0.33	3.09	1	1.33	0.011	0.117	0.622	-0.078	0.05	0.01*

Quadratic or nonlinear trend arise when a population peaks or declines in the middle of the time series, or when the population declines rapidly at the beginning or increases rapidly at the end of the time series. Blue monkeys showed a significant quadratic trend, declining form 4.8 individuals/km^2 in 1997 to 0.6 individuals/km^2 in 2007 and then rebounding to 5.2 individuals/km^2 in 2011. Angolan colobus also showed a quadratic trend remaining at densities of 1 – 5 individuals/km^2 between 1997 and 2006, and then rising quickly to 9.5 individuals/km^2 in 2011. L'Hoest's monkeys have declined slightly over time, but the trend is not significantly different from 0. Chimpanzees have fluctuated moderately, but there is no long-term trend in density.

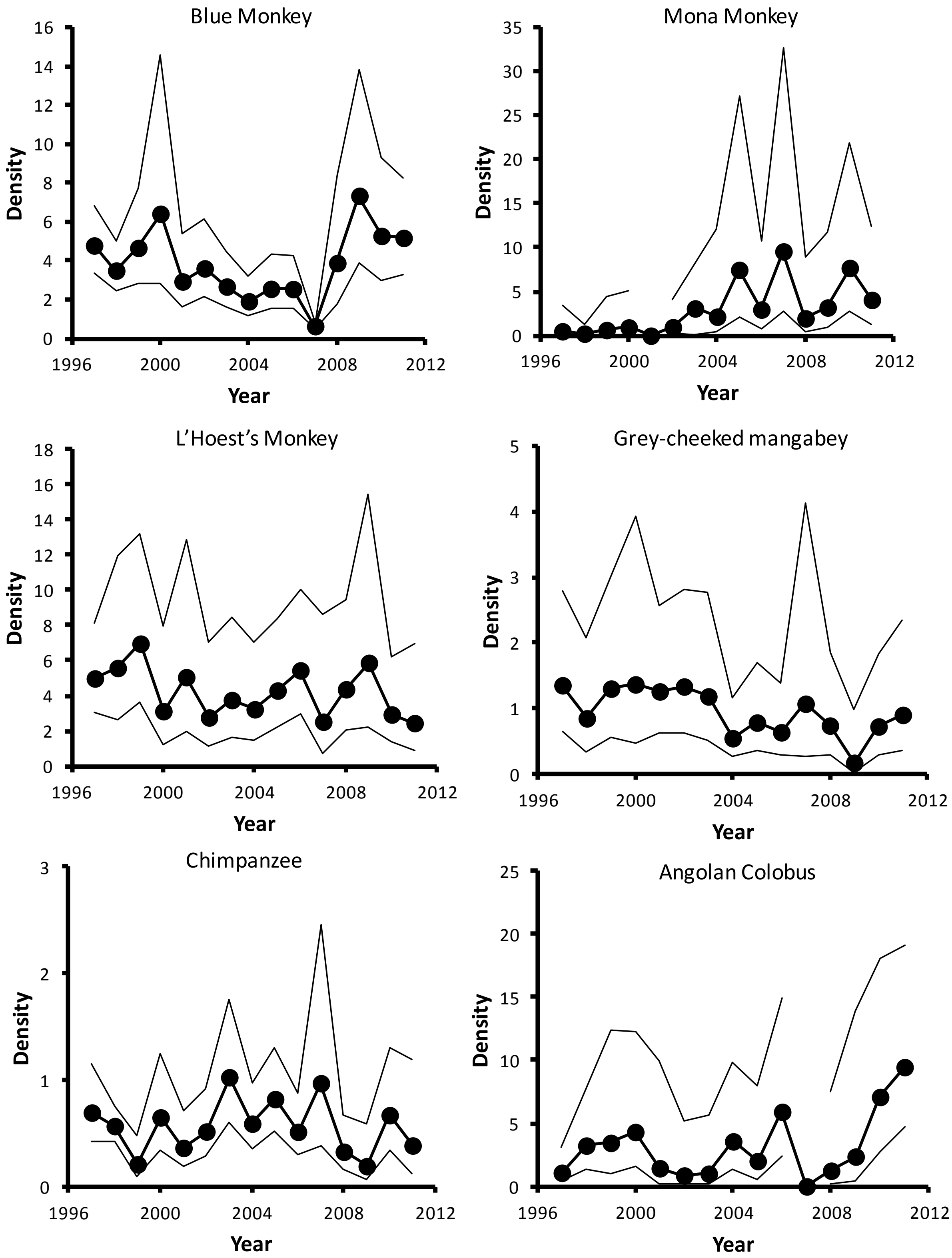


Figure 6. Density estimates, 95% confidence intervals, and trend over time for 6 primate species.

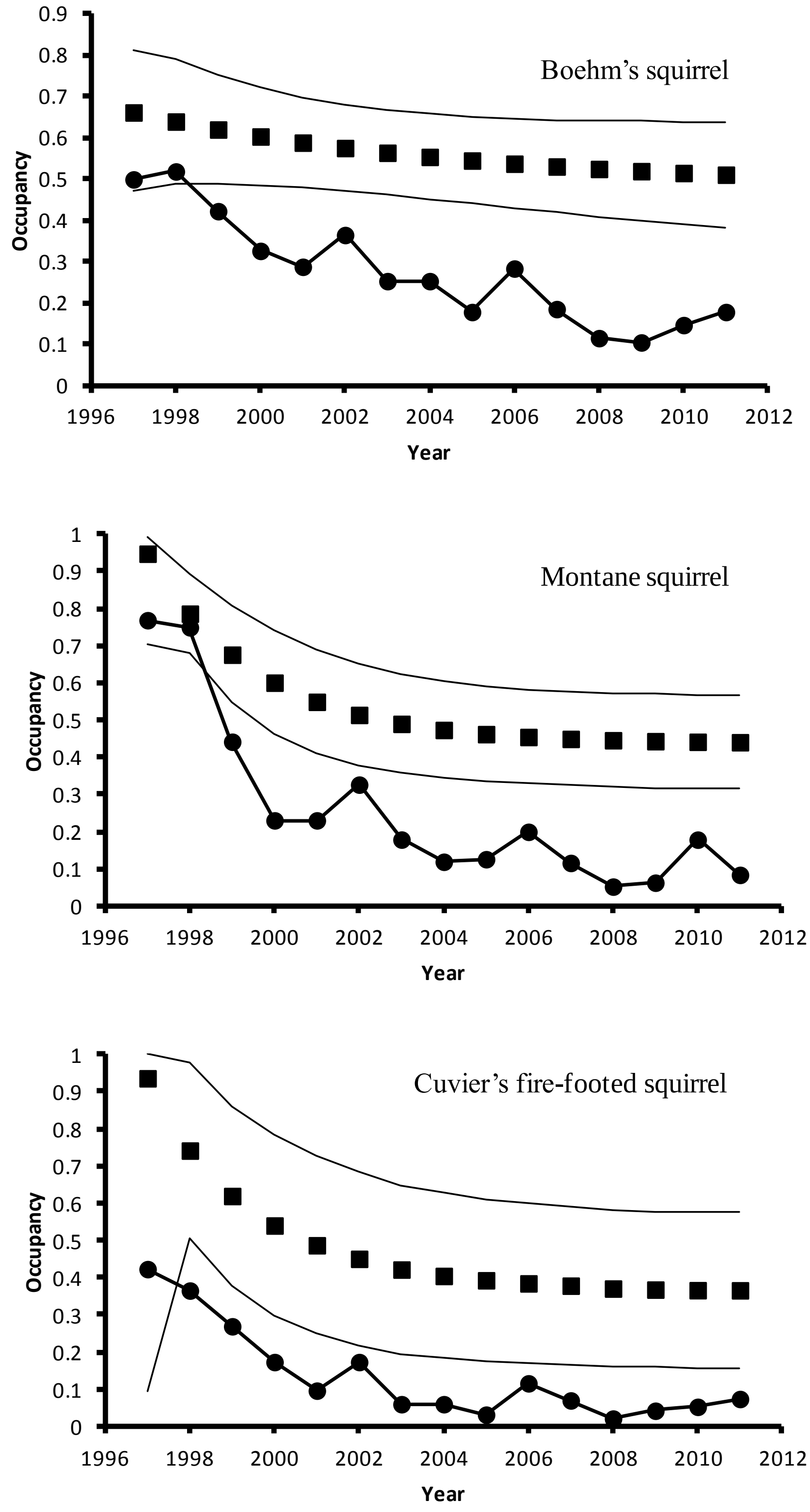


Figure 7. Observed (closed circle) and estimated occupancy (filled squares) for Boehm's squirrel, Montane sun squirrel and Cuvier's fire-footed squirrel. Estimated occupancy bounded by 95% confidence intervals.

Squirrel Distribution and Abundance

We were able to analyze three of five squirrel species encountered (Table 4, Table 6). Between 1997 and 2011, all three species contracted in distribution throughout the study area (Table 6, Figure 7). Decreases in Montane and Cuvier's fire-footed squirrels were steepest early in the monitoring period (1997 – 2001) and then became stable in later years. Boehm's squirrel displays a constant linear decline. Declines ranged from 23% in Boehm's squirrel distribution to 61% for Cuvier's fire-footed squirrel. All detection probabilities were significantly affected by the amount of effort (number of surveys) in a given year. There was support for a positive effect of elevation on occupancy through local extinction meaning that the likelihood of local extinction was higher at lower elevations, so occupancy was lower at these elevations (Table 9). For Cuvier's fire-footed squirrel, local extinction was higher at higher elevations and occupancy was lower at higher elevations. For Montane sun squirrels, local extinction was higher at high elevations and local colonization was lower at high elevations. Taken together, occupancy was lower at high elevations.

Table 9. Occupancy analysis results for squirrels.

Boehm's squirrel	AIC	ΔAIC	AIC wgt	no.Par.	Elevation	Effort
ψ,γ(),ε(),p(Effort)	2261.8	0	0.6974	5		Sig. +
ψ,γ(),ε(Elevation),p(Effort)	2263.5	1.67	0.3026	6	NS -	Sig. +
Cuvier's fire-footed squirrel						
ψ,γ(),ε(Elevation),p(Effort)	1052.1	0	0.7086	6	NS +	Sig. +
ψ,γ(),ε(),p(Effort)	1054.0	1.82	0.2852	5		Sig. +
Montane sun squirrel						
ψ,γ(),ε(Effort),p(Effort)	2016.7	0	0.4477	6		Sig. - ε, Sig. + p
ψ,γ(),ε(Effort,Elevation),p(Effort)	2017.0	0.28	0.3892	7	NS +	Sig. - ε, Sig. + p
ψ,γ(Elevation),ε(Effort),p(Effort)	2019.3	2.64	0.1196	7	NS -	Sig. - ε, Sig. + p

Squirrel densities all showed evidence of decline between 1997 and 2006-7, followed by recovery, indicated by significant quadratic effects in the time series (Table 8, Figure 8). Because squirrels tend to be solitary, most of the variation in densities is due to changes in encounter rates. Boehm's squirrel density declined from 6.4 individuals/km^2 to 3.0 individuals/km^2, before recovering to 5.25 individuals/km^2. Cuvier's fire-footed squirrel declined from 2.5 individuals/km^2 to 0.33 individuals/km^2 before recovering to 1.7 individuals/km^2. The Montane sun squirrel declined from 5.5 individuals/km^2 to 1.0 individuals/km^2 before recovering to 4.5 individuals/km^2.

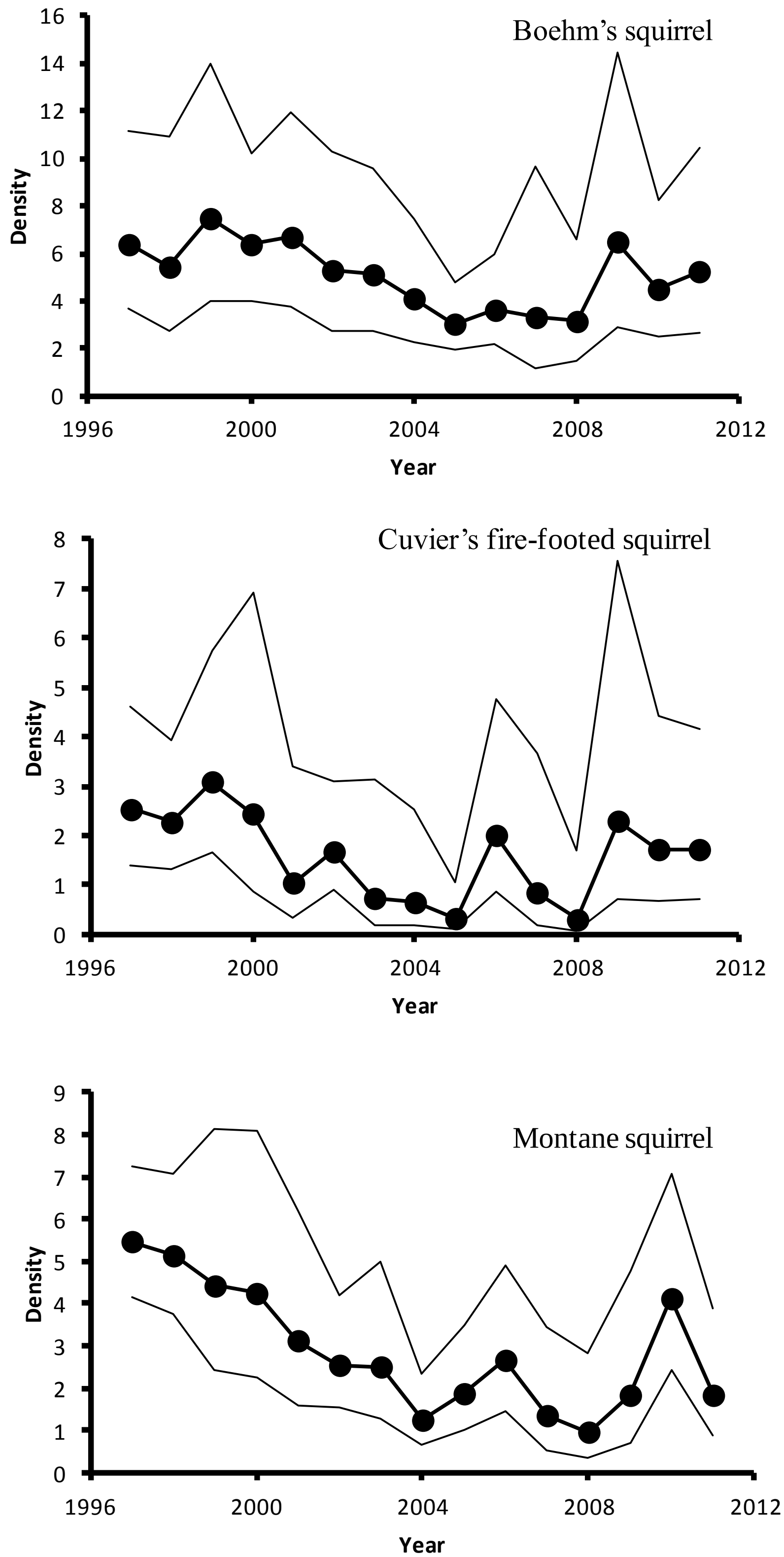


Figure 8. Density estimates, 95% confidence intervals, and trend over time for 3 squirrel species.

Terrestrial mammal distribution

We conducted occupancy analyses for duikers (Black-fronted and yellow-backed duikers combined), Brush-tailed porcupine, Bushpig and Giant pouched rat (Table 6, Figure 9). Nyungwe has three duikers, although we only detected signs that were attributed to Black-fronted and Yellow-backed duikers (n=54 observations). Yellow-backed duikers were extremely rare with only 3 confirmed sightings. Since the beginning of monitoring, duikers have been uncommon, with an estimated occupancy of just 17% of the survey area (Table 6). This has declined to approximately 5% in recent years. The simplest occupancy model was the most parsimonious, likely due to the paucity of data (Table 10).

Table 10. Occupancy analysis results for terrestrial mammals

Duikers	AIC	ΔAIC	AIC wgt	no.Par.	Year	Elevation	Effort
ψ(),γ(),p()	396.3	0	0.9488	3			
Bushpig							
ψ,γ(),ε(Year),p()	951.7	0	0.7224	17	Sig.+		
ψ,γ(),ε(Year),p(Effort)	953.7	1.93	0.2752	18	Sig.+		NS
Brush-tailed porcupine							
ψ,γ(),ε(),p(Effort)	405.5	0	1	5			Sig. +
Giant pouched rat							
ψ,γ(),ε(),p()	1042.6	0	0.2715	4			
ψ,γ(),ε(Elevation),p()	1043.1	0.52	0.2094	5		NS -	
ψ,γ(),ε(),p(Effort)	1043.3	0.7	0.1913	5			NS
ψ,γ(),ε(Elevation),p(Effort)	1043.7	1.14	0.1536	6		NS -	NS
ψ,γ(),ε(Year),p()	1044.4	1.81	0.1098	17	NS		
ψ,γ(Year),ε(),p()	1045.5	2.88	0.0643	17	Sig.		

Brush-tailed porcupine has declined only by 4% between 1997 and 2011 dropping from 25% occupancy to 21% occupancy (Table 6). Giant Pouched rats suffered a dramatic decline from 46% occupancy to 19% in the study area. No single model was strongly supported for giant pouched rats. None of the covariates carried much weight (AIC wgt for ε (Elevation) = 36.3%; p(Effort) = 34.5%), indicating that there is probably unmodeled heterogeneity in this data set (Table 10).

Bushpigs are the only terrestrial mammal that appears to be on the increase, possibly as a result of recovery from a previous population decline. Bushpigs increased occupancy in the study area from 4% in 1997 to 28% in 2010. In 2011, there appears to be a precipitous decline in bushpig occupancy. While worrisome, we cannot rule out the possibility that this is an artifact of sampling or modeling.

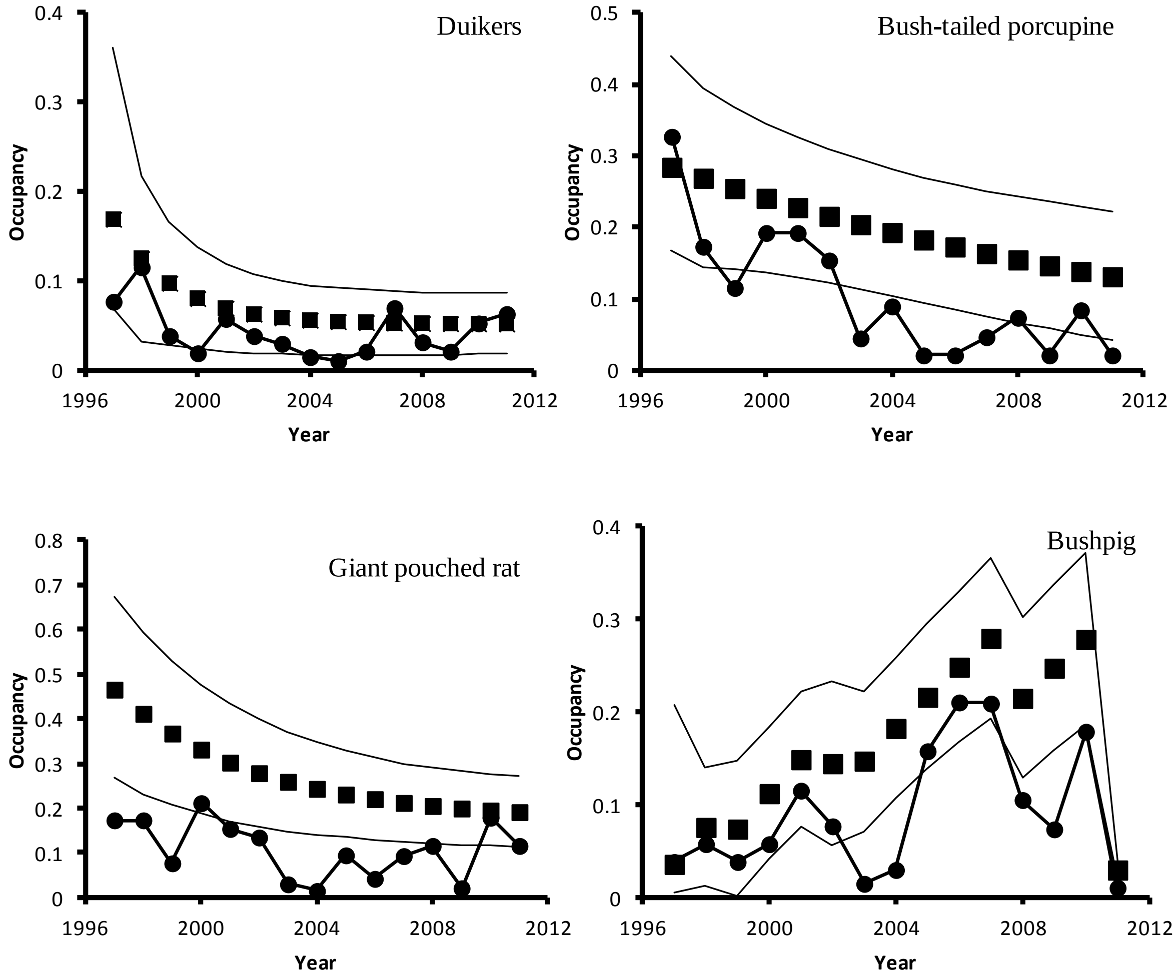


Figure 9. Observed (closed circle) and estimated occupancy (filled squares) for two species of duikers, Brush-tailed porcupine, Giant pouched rat and Bushpig. Estimated occupancy bounded by 95% confidence intervals.

Effect of sampling effort

A general result of occupancy modeling for all mammals is the important effect of sampling effort on occupancy estimates. Obviously, the more we search for uncommon species, the more likely we are to encounter them at least once during the year. The sampling effort for mammals was extremely uneven over time (Figure 10) and space, and we cannot rule out the possibility that high sampling effort in 1997/98 may have skewed the trend data toward higher occupancy and abundance earlier in the time series. Although occupancy and density modeling are robust to unequal sampling effort over time, it is not immune to unequal sampling.

A second general result is that models with an effect of elevation on the probability of local extinction were consistently chosen. Because of the modeling structure chosen, a positive effect of elevation on colonization is associated with increases in occupancy, whereas positive effects of elevation on extinction are associated with decreases in occupancy. Out of 13 analyses, 4

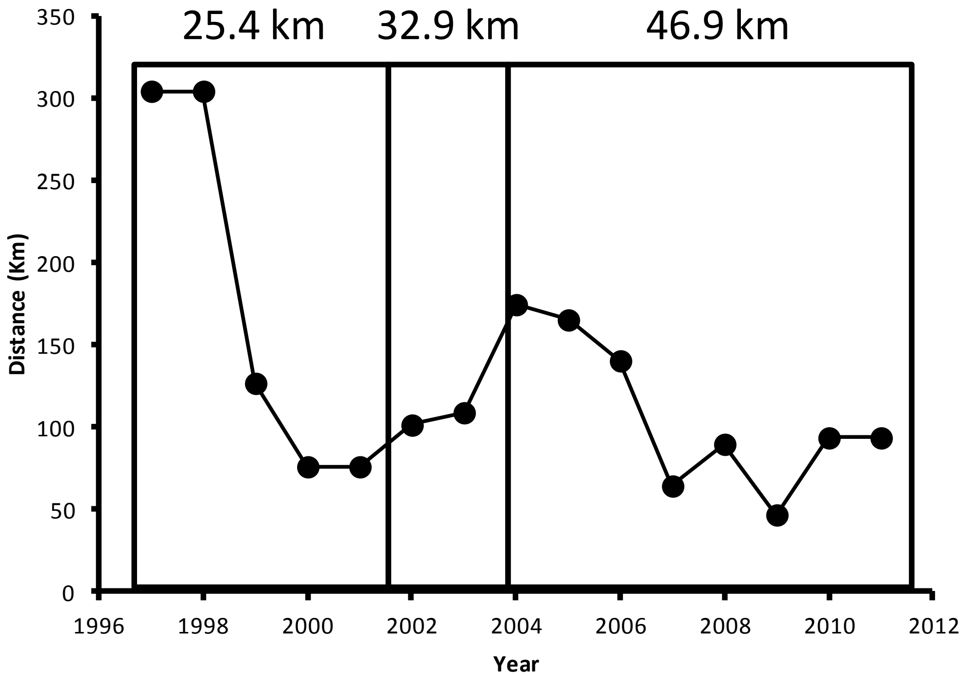


Figure 10. Kilometers of line transect survey effort per year in Nyungwe National Park. Numbers monthly total kilometers per survey and boxes indicate time period for the level of monthly effort.

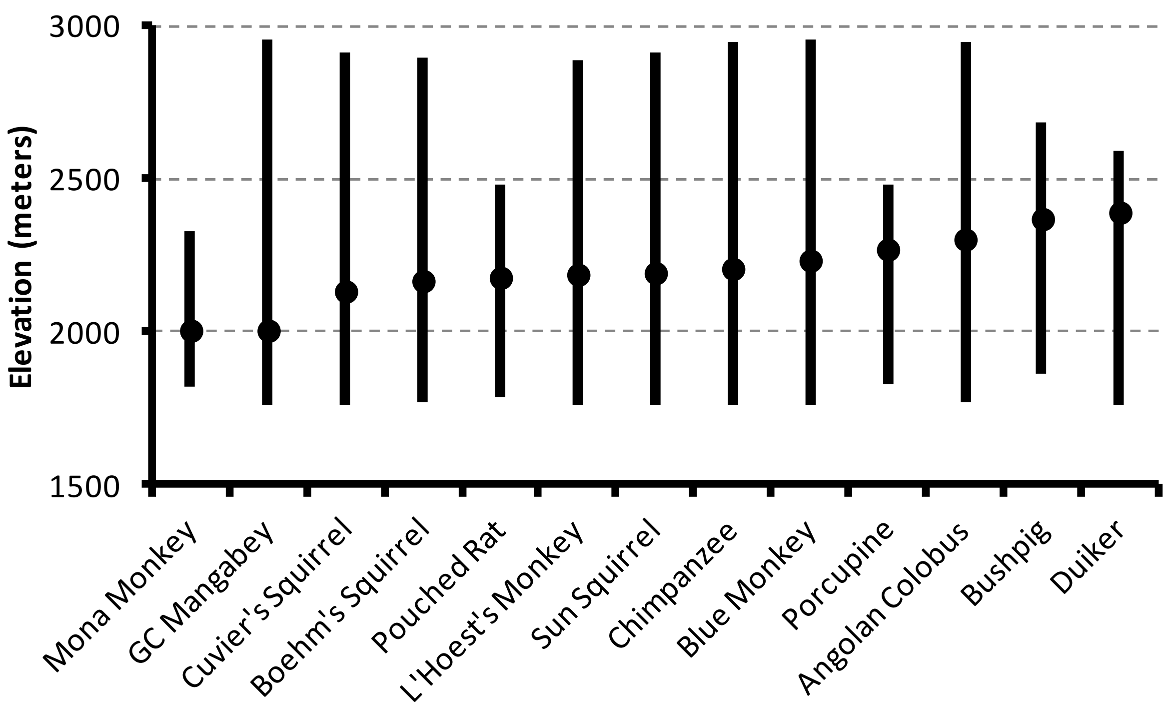


Figure 11. Distribution minimum, maximum, and average (closed circle) elevation by species.

species had no elevation effects (Mona monkey, duikers, bush-tailed porcupine and bushpig). Each of these species had skewed elevation distributions (Figure 11), with most observations near the minimum (Mona monkey) elevation, or the maximum elevation (duikers), suggesting restricted elevation distributions. These four species also shared elevation ranges of less than 1,000 m. Of the remaining species, most were found at all elevations (range > 1,100 m), except the Giant pouched rat, which was restricted to a 690 m range of elevation. Of the 9 species with elevation effects on extinction, 6 species had positive effects on extinction, meaning that occupancy tended to decline at higher elevations, and 3 species had negative effects, meaning occupancy tended to decline at lower elevations. Only Mona monkey showed a positive effect of elevation on colonization and only Montane sun squirrel showed a negative effect of elevation on colonization.

DISCUSSION: Mammals

The general trend for distribution of mammal populations in Nyungwe NP is decline. Among terrestrial mammals and squirrels, declines in distribution within the study area between 1996 and 2011 range from 17% for Bush-tailed porcupine to 70% for combined duiker species. Only the Bushpig shows an increasing trend in occupancy. Among primates, reductions in distribution range from 27% for Blue monkeys to 46% for Eastern chimpanzees. Only the Angolan colobus showed an increasing trend in distribution within the study area.

The general trend in detection probability for mammals is also a decline over time. Most species were becoming harder to detect in the later years. Sampling effort had a significant and positive effect on detection probabilities for all primates except the Mona monkey, all squirrels and the bush-tailed porcupine. This makes sense because the more months that are sampled, the more likely we are to observe species that might make seasonal movements into and out of the study area. Unfortunately, the sampling effort also has an associated time trend because sampling was more intensive in the early part of the monitoring program. This confounds interpretations about declines.

Among primates, Eastern chimpanzee and L’Hoesti monkeys showed no time trend in density suggesting that density has been relatively stable over time. Mona Monkey density has increased steadily over time, primarily due to increasing encounter rates. Angolan colobus monkeys also have increased over time, especially between 2008 and 2011. The Angolan colobus is the only species to show both an increase in distribution and in density. Blue monkeys declined steadily between 1997 and 2007 but appear to be on the increase after 2007. The decline was due to a reduction in group size over time. Only the Grey-cheeked mangabey has declined significantly over time, from 2.8 individuals/km^2 to 1.8 individuals/km^2 in 2011. The reason for this decline is unknown.

Squirrel densities all declined between 1997 and 2005 and then all species showed signs of recovery. It is possible that squirrels were hunted to very low densities and then hunters switched to other rodents.

Unfortunately, we cannot use the mammal data to directly address the question of whether intensification of patrol efforts has resulted in improved wildlife populations. First, the monitoring design does not match well spatially with the allocation of patrol effort. Therefore, the sampling area is not necessarily representative of the area where we want to make inferences. Second, there is a confounding of sampling effort and time. As patrol efforts improved over time, monthly sampling effort for monitoring declined. Because of small sample sizes, we were forced to consider 1 year as the temporal sampling unit. This calls into question whether the changes in abundance were due to animals moving into and out of the study area over the course of a year, a violation of population closure assumptions.

The data, however, indicate that abundance and distribution of terrestrial mammals squirrels and primates improved at the same time that patrol efforts intensified, indicating some positive effect of patrol. Clearly hunting, especially use of snares, is the most likely culprit in the widespread decline of squirrels and terrestrial mammals in the park. Snares are non-selective, meaning that semi-terrestrial primates can be unintentional targets as well as the terrestrial mammals. Arguably, the recovery of squirrels may be a function of snare removal activities. However, between 2006 and 2010, the time of squirrel recovery, snare removal per kilometer of patrol has stayed relatively constant. , For species that declined in the early part of the surveys and then recovered, the timing of recovery is after 2003 when patrol efforts intensified. The data also show declining trends in some primate populations that are not normally hunted in Nyungwe. So while patrol efforts have improved, it is unclear that the improvement has translated into consistent improvements in wildlife distribution and abundance.

NYUNGWE NATIONAL PARK BIRDS

Nyungwe National Park (NNP) is an important conservation site for birds, in particular due to the high number of range-restricted species, regional endemics and globally threatened species. In total, NNP protects more than 319 species of bird (Chao, 2008; unpublished data), of which 26 are Albertine Rift endemics. In order to ensure long term conservation of birds in Nyungwe Forest, Chao *et al*. (2012) pointed out that an understanding of bird population densities, distributions and ecological requirements was needed. Chao *et al*. (2012) presented encounter rate data from NNP bird surveys between 1995 and 2006, and described the habitat and altitudinal associations of many species.

Despite its importance, ornithological research in NNP has been rare (Chao *et al*. 2012). Only Chin Sun conducted research on birds, targeting foraging ecology of three species of turaco, the Great-blue, Ruwenzori and Black-billed turacos (Sun & Moermond, 1997; Sun *et al*., 1997). Birds have also been included in a number of surveys. General bird and mammal surveys were conducted by Storz (1982) and Vedder (1988). R. J. Dowsett conducted the first systematic bird survey in NNP (Dowsett, 1990; Dowsett *et al*., 1990), recording a total of 275 species. Plumptre *et al*. (2002) conducted a parkwide biodiversity survey in 1999 and recorded 196 species. A second biodiversity survey was completed in 2009 (Chao *et al*., 2010). There have been no documented bird extinctions in the park.

The bird community of Nyungwe NP hosts species that are considered lowland specialists with upper elevation limits within Nyungwe NP, montane specialists with their entire elevation range within Nyungwe NP, and montane specialists with lower elevation limit within Nyungwe NP. Chao *et al.* (2010) suggested that, based on the work of Picton-Phillipps and Seimon (2010), that changing climate in the Nyungwe NP "*would promote upward range extensions and downhill range contractions among numerous taxa with a net upward migration*".

The Nyungwe National Park Management Plan 2012-2021 (2012) considers conservation of Nyungwe's birds, especially the Albertine Rift endemics and raptors, as important conservation targets, and requires information on bird communities in NNP. Here we present the results of trends in bird diversity and abundance between 1997 and 2011 in NNP. We pay special attention the trends in distribution and abundance along the elevation gradient as these may give clues to the effects of climate change on bird distribution in Nyungwe NP.

METHODS: Birds

Bird surveys were conducted From 1997 to 2011 (Table 3) along transects that range in length from 1.3 to 4.5 km, with point count stations set up at 100 m intervals along the transects (Figure 1, Table 2, 3). Survey effort was variable over time and space. At the Uwinka and Gisakura sites, count stations on transects of 2 km or less were surveyed each time the transect was surveyed. On the longer transects, only half of the stations were surveyed on a given visit. In Cyamudongo, half of the stations on a transect were surveyed on a given visit irrespective of transect length. At Busoro, Gasare and Uwasnkoko sites, all count stations were surveyed on each transect survey. At each point count station, observers waited for 2 minutes to allow birds to settle and then recorded all sightings and calls of birds for a period of 10 minutes. Distances to birds that were visible were measured using a laser rangefinder out to 70 m and estimated for distances greater than 70 m. For birds detected by calls, all distances were estimated. Detection cue is noted (vocal, visual, flying), as are behaviors at time of observation (flying, sitting, etc.) and species of tree in which the bird is active (if relevant). Phenological state of trees near the point count station are also noted. All transects start from a road or base camp and are oriented into the park. As a result, altitude and distance from road are highly correlated on most transects.

The sampling effort generated totaling 82,969 observations of 206 species over 15 years. Because we had so much more data, we were able to attempt to control for differences in sampling effort. Due to the difference in effort over time (Figure 12), we risk confounding detection probability with sampling effort. In species richness sampling, the number of species encountered tends to increase with sampling effort. This is clear in the Nyungwe bird data (Figure 13). Between 1997 and 2004, sampling effort declined over time and the number of species detected declined. After the expansion of surveys increased the spatial coverage, new habitats were added that included species not previously recorded and the species counts rose again. Overall, sampling effort and species detected were significantly associated ($r = 0.63$, $P < 0.05$). If we consider only the original 10 survey transects, we find that for every 100 points of sampling effort, we pick up 2 rare species that would otherwise be missed ($r^2 = 0.81$, $P<0.01$).

To reduce problems associated with changing sampling effort, spatial extent, and habitat coverage, we analyzed the original 10 transects covering 1997 to 2011, separately from the

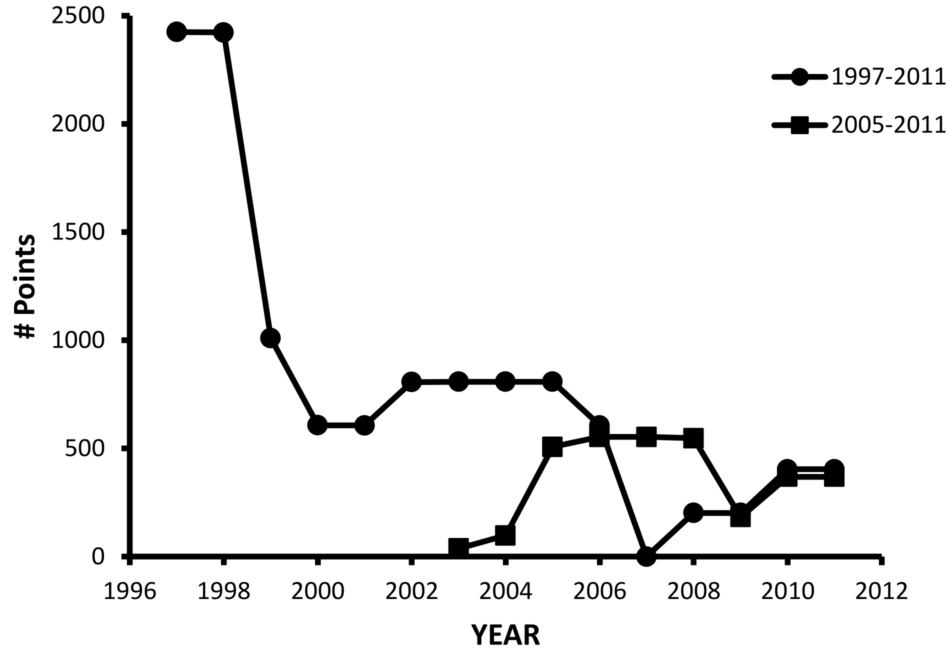


Figure 12. Variation in point count sampling effort over time (# points surveyed) for Nyungwe bird surveys for 1997 – 2011 dataset and 2005 – 2011 dataset. In the latter, 2003 and 2004 were dropped from analyses due to low survey effort.

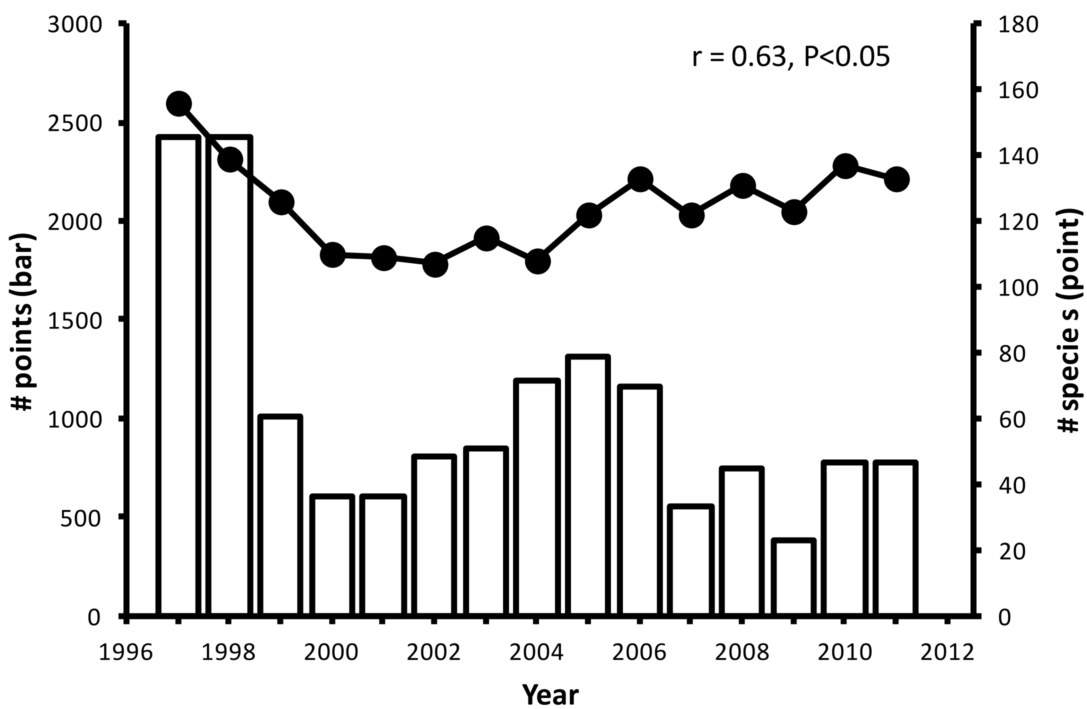


Figure 13. The relationship between sampling effort and number of species detected in a year.

dataset for transects added in 2003 and 2005. For the species richness calculations, we considered a maximum of 6 months of samples in any given year. We also drop the 2003 and 2004 data from Cyamudongo due to insufficient sampling effort (< 100 points/year). Finally, because data were collected in only one month in 2009, we combined the 2008 and 2009 data. We will refer to the longer time series as the 1997 dataset and the shorter time series as the 2005 dataset. For each dataset, we calculated species richness over time, species-specific density estimates for those species with sufficient data, and relative abundance indices (encounters per point count) as basic metrics.

Species Richness

We used occupancy-based multi-season models (MacKenzie *et al*., 2006) of relative species richness to evaluate trends in species richness in the 1997 data set and the 2005 data set (O'Brien *et al*., 2010). Relative species richness (RSR) is the proportion of species occurring in the region that are estimated to occur in the study area. Regional species lists are records of all the species that have been identified in the vicinity of the study site and represent a history of occurrence. A regional species list may or may not be an accurate representation of the species occurring in the region at the time of a survey. RSR is a snapshot of the proportion of species that currently reside in the study area. Occupancy based methods are well-suited for species richness estimation because they allow the direct incorporation of covariates that might affect species richness and the detection of species. Occupancy-based methods also are robust to variation in sampling effort. Unequal sampling effort increases the variance but does not affect the estimate.

We approached the analysis using a multi-season method that allows species to appear (colonize) and disappear (local extinction) seasonally. As an example, suppose that we sample for 2 seasons, S1 and S2. Sampling is replicated x times within S1 and S2. Within a season, a species is assumed to be present or absent in the study area and does not change status. Between seasons, a species that was absent in S1 can appear in the study area (local colonization) or a species that was present in S1 can disappear (local extinction). The three parameters (proportion of species present in S1, probability of colonization and probability of extinction) describe the dynamics of species richness between the 2 seasons and lead to an estimate of RSR for S2. This simple example can be extended for many seasons (or years) to develop a history of changes in species richness over time and factors that might influence those changes.

As in the mammal distribution estimation, models can be developed (parameterized) in a number of ways. For example:

1. $\varphi(.)\varepsilon(.)\gamma(.)p(.)$: In this model RSR (denoted by φ), local extinction (denoted by ε), local colonization (denoted by γ) and detection probability (denoted by p) are all constant throughout the analysis.

2. $\varphi(.)\varepsilon(.)\gamma(.)p(\text{YEAR})$: In this model, RSR in S1, extinction and colonization are constant but p varies between seasons. φ, ε, and γ are calculated directly and RSR in S2 is calculated from φ, ε, and γ.

3. $\varphi(\text{YEAR})\gamma(.)p(.)$: This model estimates φ for S1 and S2 directly, estimates γ and p directly, and calculates ε from the φ's and γ.

Many more models are possible. It is also possible to incorporate covariates into estimation. For example Model φ(HABITAT)ε(.)γ(.)p(YEAR,EFFORT) would estimate RSR as a function of different habitats where species might be found, and estimates p as a function of sampling year and sampling effort in the replicate.

In this analysis, we considered fairly simple models. We used a regional bird list of 319 species observed in Nyungwe on surveys and compiled from other activities (Chao, 2008; unpublished data). Detection probabilities of different bird species were either constant or varied by body size. The time series of estimates for φ were generated from a set of models that considered combinations of φ, ε, and γ to be a function of time (YEAR) and effort (EFFORT). Data were structured for 6 monthly replications for the 1997 data set (Table 11) and we used missing values for years with less than 6 months of sampling. For the 2005 dataset, we considered 3 replications and used missing values in years with less than 3 monthly surveys. We evaluated 14 models and used AIC criteria (Burnham and Anderson 2002) to rank models in order of likely support. We retained models with AIC weights >0.05 for further consideration. If more than 1 model met the AIC criteria, we used model averaging to develop final parameter estimates. Finally, we estimated the stability of community composition over time and between data sets using the Sorenson similarity index.

Table 11. Schedule of monthly point count sampling for birds used in the species richness analysis for Nyungwe Forest Reserve. X's in bold indicate months that were combined between years to generate a dataset.

	1997-2011 Data												2005-2011 Data											
Year	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
1997	X			X	X		X	X		X														
1998	X			X	X		X	X		X														
1999	X	X	X	X	X																			
2000	X						X			X														
2001	X			X			X																	
2002	X			X			X			X														
2003	X			X			X			X														
2004	X			X			X	X		X	X													
2005	X			X			X			X			X			X			X	X		X	X	
2006	X			X			X						X	X		X	X		X	X				
2007																	X			X			X	
2008								**X**						X			X			**X**				
2009		**X**												**X**										
2010		X						X						X						X				
2011		X						X						X						X				

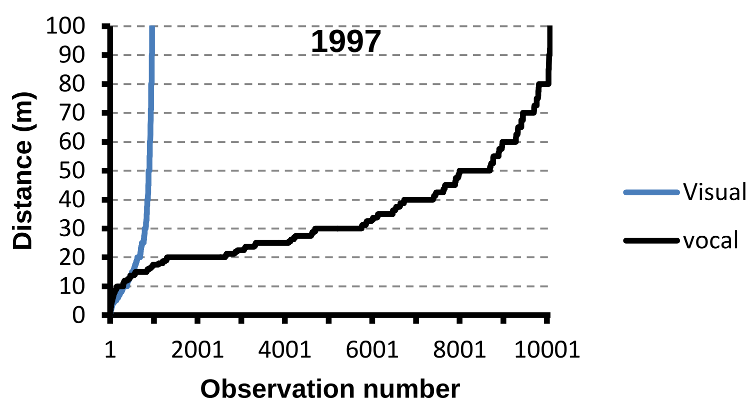
Encounter Rates and Density Estimation

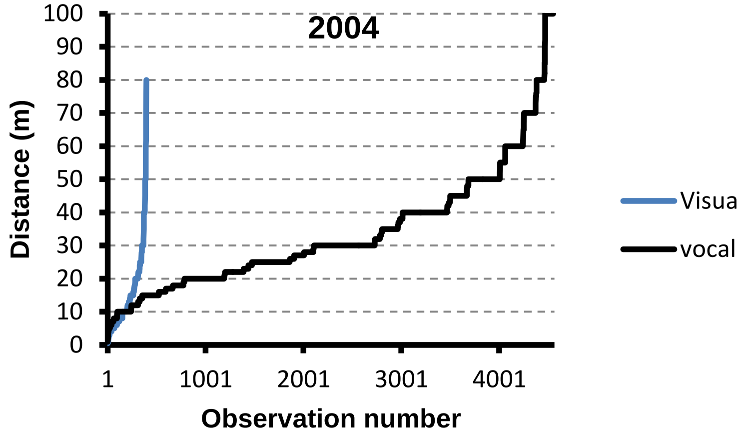
We used variable point count methods to estimate densities of birds over time in Nyungwe NP to correct observations for detection probability. Point count surveys are a non-invasive, cost effective method of monitoring bird populations. To implement a point count survey, an observer positions himself at a sampling point and, during a fixed recording period, the observer records the distance between himself and any bird he observes (Buckland, 1987, 2006; Buckland *et al*., 2008) out to a fixed distance or to infinity. At the end of this period, the observer moves to the next point and repeats the exercise until all points have been visited. In circular plots, the area between radial distances *r* and 2*r* is three times greater than that between 0 and *r*. Detections of birds therefore usually increase from the center out to some distance *d* and then begin to decline.

To implement distance-based density estimation, we require that a few assumption be met: (1) birds are randomly distributed throughout the study area; (2) birds at the observation point are detected with probability $p = 1$; (3) birds remain stationary during the observation period; (4) distances are recorded without error or birds are assigned to grouped distances without error; (5) observations are independent events; (6) no animal is counted more than once; and (7) if birds occur in clusters, clusters are recorded accurately. Assumption 1 can be met by randomizing the point locations or by randomizing the starting point for a systematically spaced set of points. To minimize the effects of failure of Assumption 3, the observer usually allows a few minutes after arriving at a point for birds to adjust to his presence. Note that birds flying through the point are not recorded. Assumption 4, the exact measurement of distances, is the most difficult to meet. Often, we rely on visual and auditory cues for detection and these processes may generate different detection distributions. Aural detections are harder to measure precisely. Because area increases with the square of radial distance, measurement errors produce more severe bias in point count surveys than in line transect surveys. Finally, multi-species surveys are hard to implement well because we are coping with a range of species that have different detectabilities and it is difficult to find robust methods that give low bias across a wide range of species.

In reviewing the sampling design for the Nyungwe bird survey, we were satisfied that the assumptions were either met or were not seriously violated except for assumption 4, measurement accuracy. Often, distances are estimated and accuracy of the estimations decreases with increasing distance. This leads to a phenomenon called ‘heaping’ where distances are rounded off to 5 or 10 m intervals. Often, distances are accurately estimated out to 30 – 40 m, then 5 m roundoffs begin, followed by 10 m roundoffs. In the Nyungwe surveys, the observers carried laser rangefinders, accurate to 70 m to measure observer-bird distance, which should have ensured accurate distance measurements. But because cues included both visual and aural detections, measurement error required evaluation. We plotted the distribution of detection for visual and aural cues (Figure 14) out to 100m for three years of surveys (1997, 2004 and 2011) to assess the whether there was evidence of heaping. If rangefinders were used consistently, we expected heaping to occur between 70 and 100 m. Aural cues dominated each dataset (91% - 93% of observations). The visual observations showed little evidence of heaping. Aural observations showed a significant effect of heaping, in the form of a step-shaped distribution. Furthermore, heaping was evident at 20 m. and become more severe with increasing distances and over time. By 2004, most observations at 40 m and beyond were clumped into 10 m intervals, despite use of rangefinders. Observers did not improve in their ability to estimate distances over time.

When significant heaping occurs, there are two solutions. First is to group distances into bins that mirror the heaping, develop the detection curve using the grouped data and estimate density using Distance sampling models (Thomas *et al*., 2010). A second approach is to reduce the distances classes to two groups, being less than, or greater than a specified value r_0 (Buckland, 1987). Since there are only two groups of data, the sampling distribution is binomial. Binomial models are sometimes used as indices of abundance to assess changes in abundance over time and over space, and are especially useful for multi-species surveys. Buckland (1987) developed a half-normal binomial model for point transects that has an analytical solution. We used the binomial model for this analysis both because of the appropriateness for multi-species surveys and the ease of analysis. The half normal binomial model can be implemented using DISTANCE software or computed in an EXCEL spreadsheet.





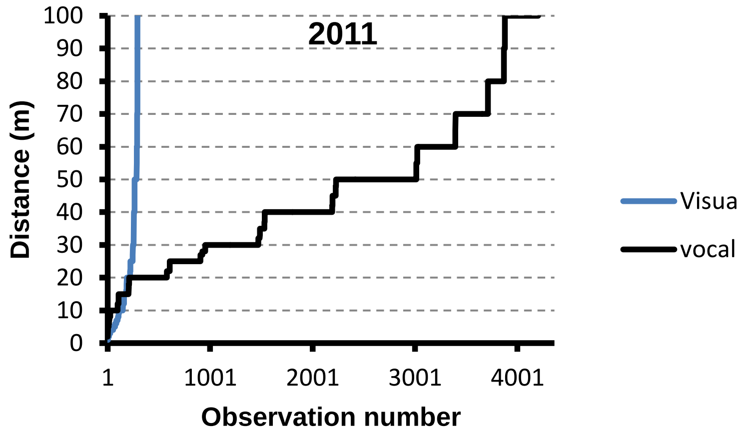


Figure 14. Distribution of observation distances for visual and aural cues in 1997, 2004 and 2011. The step-shaped distributions for aural cues indicate heaping of aural observations is significant and begins at 20 m.

We estimated density in the 1997 dataset by species for those species with more than 500 observations in the 15 year dataset. For species with less than 500 observations, we grouped species by family and estimated density for families with more than 500 observations under the assumption that species within families would share similar detection characteristics. Densities were then assigned to each species based on the number of observations per species. For the 2005 dataset we used a 250 observation cutoff for species and for families of species. Densities were computed twice using the mean observation distance for r_0 and the median distance for r_0. The goodness of fit was assessed by comparing the ratio of the mean to median estimates. Fit was judged to be good if the ratio was between 0.8 and 1.2, medium if the ratio was between 0.6 – 0.8 or 1.2 – 1.4. Otherwise the fit was considered poor. Final density was calculated as the average of the mean and median estimates. We also split the density for the 1997 dataset between observations made below and above the mean elevation in the survey 2,350 m. Because we had fewer data for the 2005 dataset, we did not calculate low and high elevation trends in density.

RESULTS: Birds

Species Richness: 1997 – 2011 Data

During surveys on the original 10 transects, we observed 208 species over 14 years (no data collected in 2007: observed RSR = 0.65) though not all species were seen in all years (Figure 15). Twenty nine species (14%) were observed only during a single year and 74 species (36%) were seen in 5 years or less. The most common species were seen in 10 - 14 years (50%).

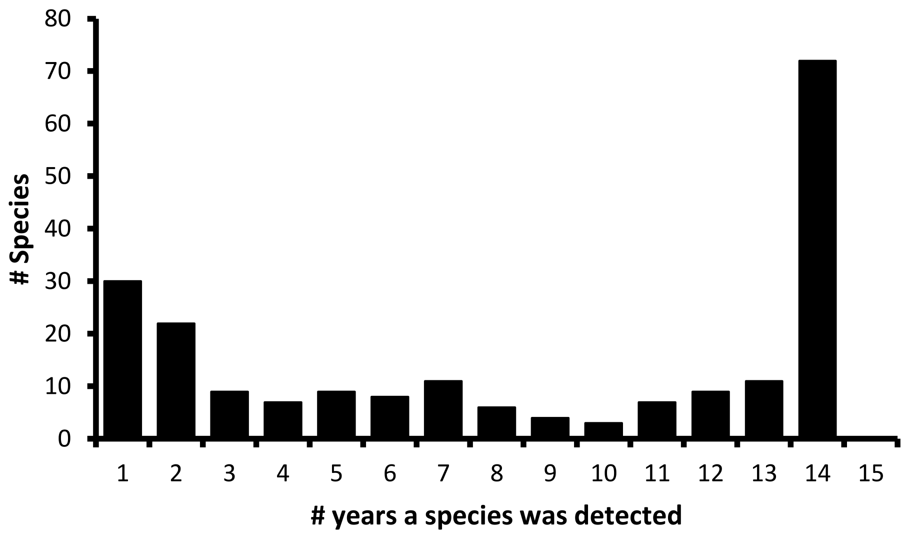


Figure 15. Number of years that a species was observed during the 1997-2011 surveys.

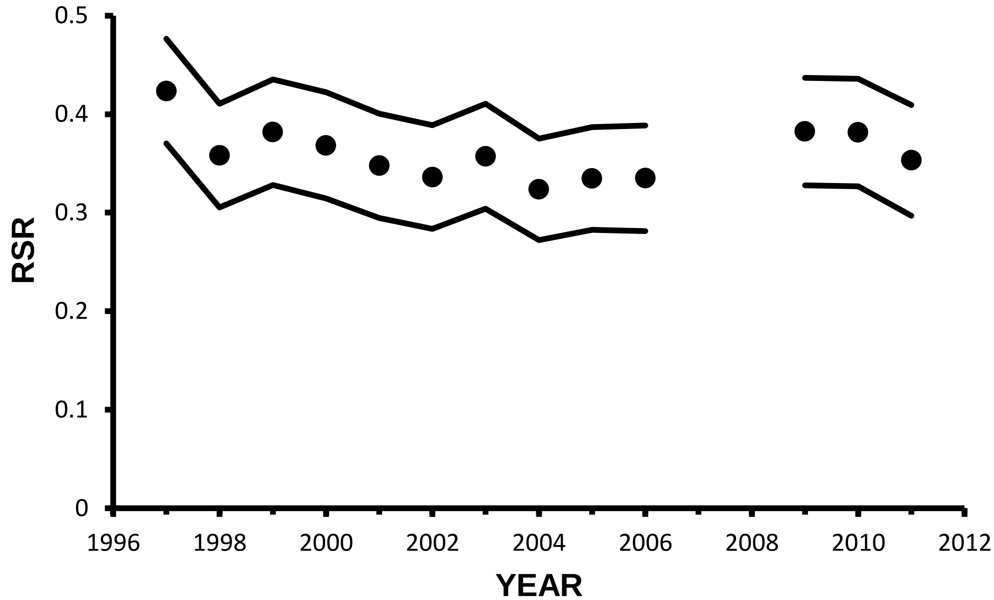


Figure 16. Relative species richness (RSR in closed circles, 95% confidence interval in solid lines) for the 1997 - 2011 Nyungwe dataset

The model with the most support was Model $\varphi(.)\varepsilon(\text{Time})\gamma(\text{Time})p(.)$ with an AIC weight = 0.9898. No other model was supported. This model holds detection probability constant over time ($p = 0.707 \pm 0.0064$), and estimated φ_1 for the first year (0.424 ± 0.0277) and subsequent φ_{time} from time-specific estimates of colonization and extinction. Annual estimates of RSR range from 0.324 to 0.424 (Figure 16). Species richness declined between 1997 and 2004, then rose again. The linear trend for the 15 years is flat however (slope = -0.0015, $r^2 = 0.06$) indicating no change in species richness over time. On average, 115 ($\pm$ 8.7) species are present in the study area in a given year.

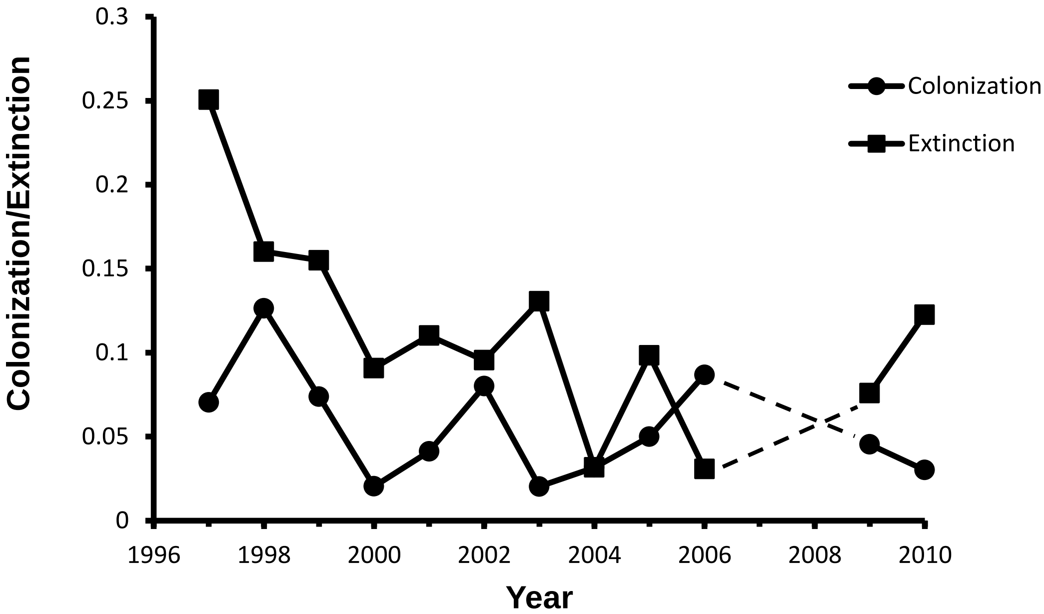


Figure 17. Probabilities of local species colonization (filled circles) and local extinction (filled squares) over time. Dashed lines indicate no estimates were available

Both colonization and local extinction declined over time (Figure 17). Extinction exceeded colonization in most years, contributing to a slight decline in RSR in RSR between 1997 and 2006, followed by recovery. Both extinction and colonization rates are fairly low and the net effect of colonization and extinction was balanced over time so that species richness remained stable. Much of the variability is likely due to sampling error for rare species.

Finally we can compare the rate of change in species richness over time (λ) a measure of community stability (Figure 18). When λ = 1.0, we conclude that there has been no change in species richness during the interval. In Figure 18, λ is significantly less than 1 in the 1997-98 interval and in the 2003-04 interval. λ is significantly greater than 1 in 2006-07. On average, however, species richness is stable across time (λ = 0.993, [0.903-1.077]). Year-to-year similarity averaged 86% (range = 85% to 90%) meaning that the species composition has remained relatively stable over time and the turnover is primarily due to occasional occurrence and disappearance of many rare species.

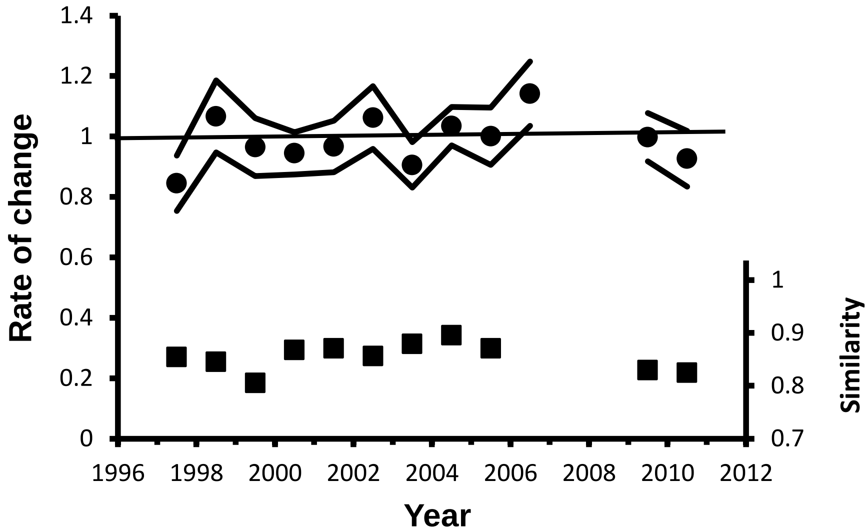


Figure 18. Rate of change in species richness over time (filled circles), 95% confidence intervals and community similarity between years (filled squares). Straight line indicates λ = 1.0 or no change.

Species Richness: 2005 – 2011 Data

Surveys in the Cyamudongo Forest began in December 2003. Six surveys were conducted in 2004 but this represented 3 complete surveys preliminary analysis showed very poor representation of bird species in those samples (49 species recorded) during 5 months of surveys). Subsequently, we dropped these years from analysis. During surveys on the latter 10 transects (2005 - 2011), we observed 157 species over 7 years (observed RSR = 0.49) though not all species were seen in all years (Figure 19). Thirteen species (8%) were observed only during a single year and 92 species (59%) were seen in all years.

The model with the most support was Model φ(.)ε(.)γ(Time)p(.) with AIC weight = 0.9802. No other model was supported. This model holds detection probability constant over time (p = 0.651 $\pm$ 0.0096), and estimated φ_1 for the first year (0.333 $\pm$ 0.0263), extinction constant (ε = 0.0531 $\pm$ 0.0096) and subsequent φ from time-specific estimates of colonization and extinction. Annual estimates of RSR range from 0.392 to 0.413 (Figure 20). Species richness increased between 2005 and 2006, then remained stable. The linear trend for the 7 years increases over time (slope = 0.0087, r^2 = 0.462). However, removing 2005 from the analysis results in a flat trend (slope =0.0018, r^2 = 0.19). On average, 125 ($\pm$ 8.8) species are present in the study area in a given year.

Colonization declined over time (Figure 21) from a high of 0.118 to 0.022. Extinction was estimated to remain unchanged over time (ε = 0.0531). On average, colonization equaled extinction, and the net effect of colonization and extinction was balanced over time so that net species richness remained relatively stable. As in the larger dataset, much of the variability is due to rare species appearing and disappearing over time.

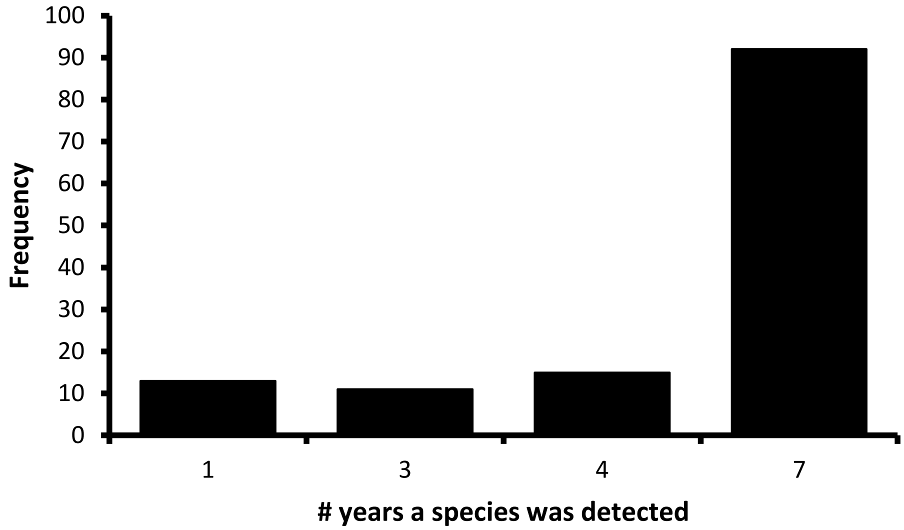


Figure 19. Number of years that a species was observed during the 2005-2011 surveys.

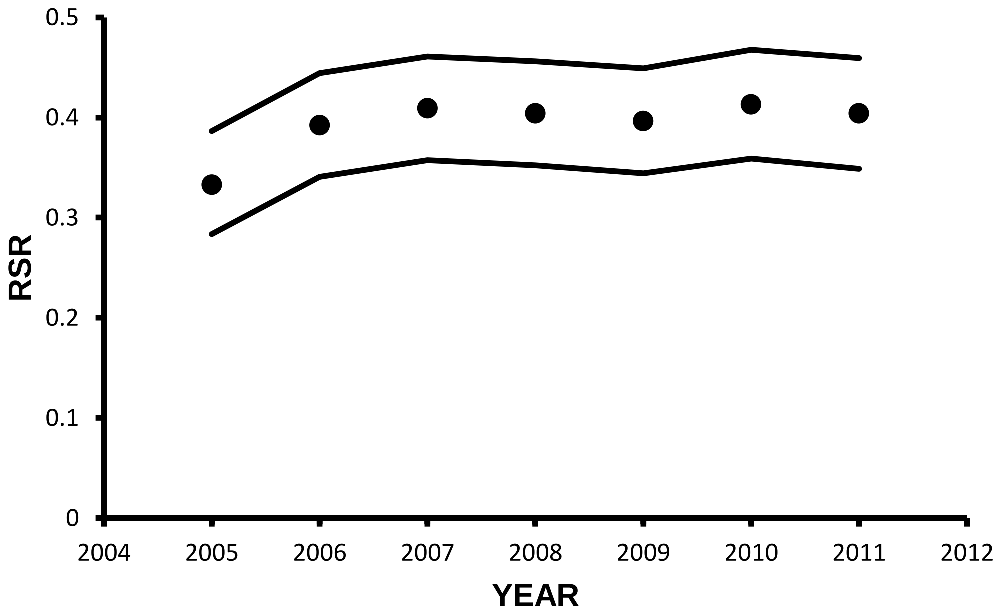


Figure 20. Relative species richness (RSR in closed circles, 95% confidence interval in solid lines) for 2005 - 2011 Nyungwe dataset.

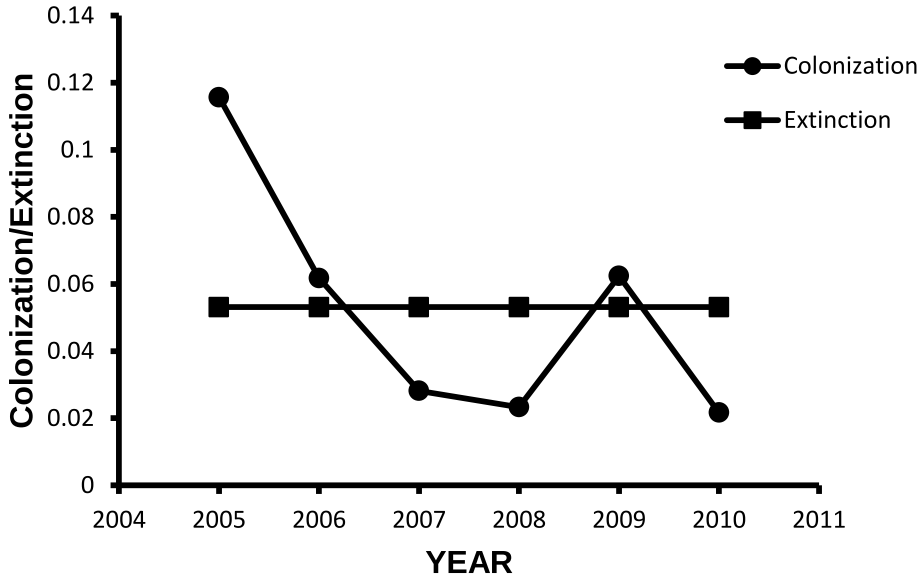


Figure 21. Probabilities of colonization (filled circles) and extinction (filled squares) over time for the 7 year dataset.

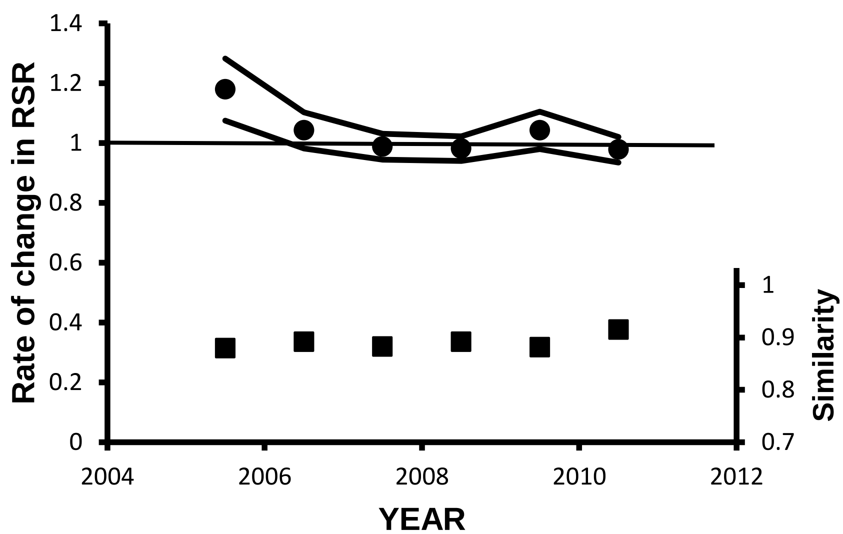


Figure 22. Rate of change in Relative species richness (λ) for 7-year dataset.

Comparing the rate of change in species richness over time, λ is significantly greater than 1 in the 2005 - 2006 interval, due to very high colonization. On average, however, species richness is stable across time (λ = 1.03, [1.18 - 0.98]). Year-to-year similarity averaged 89% (range = 88%

to 91%) meaning that the species composition has remained very stable over time and the turnover is primarily due to occasional occurrence and disappearance of many rare species.

The 1997-2011 and 2005-2011 share a similar elevation gradient, but the 2005-2011 surveys were developed to include a broader range of habitats. Between data sets, similarity was uniformly high, ranging from 0.86 in 2005 (maximum sampling effort) to 0.80 in 2008 and 2011. This means that in any given year, the 2 survey samples share $\geq$ 80% of species.

We next looked at the species that were not shared to try to distinguish sampling error from true absence. We assumed that birds that are observed in a given year at a single site but switch sites over time are examples of sampling error (present but not detected). We also assumed that species that occurred less than 3 times at a site in the 6 years were very rare and subject to sampling error. This resulted in a list of 23 species that appear to have no overlap between the datasets. Five species are unique to the 1997-2011 dataset and 18 species are unique to the 2005-2011 dataset. Finally, we eliminated species that were seen in the 2005 – 2011 dataset and in the 1997-2011 dataset but prior to 2005. Four species (Speckled mousebird, Grauer's rush warbler, Ross' turaco, and African sand martin) were found only in the 2005-2011 dataset. An additional 8 species were rare in the 1997-2011 dataset prior to 2005 (Green coucal, Black crake, Malachite sunbird, Yellow-billed duck, Hadada ibis, Black-headed waxbill, Stoenchat and African Citril). The Yellowbill (listed as Green coucal) and Ross' turaco were only observed in the Cyamudongo Forest during surveys, although we recently observed the Yellowbill near Gisakura. The remaining species are found along the Gasare and Uwasenko transects and are all species that prefer open areas, especially wetland areas.

It is difficult to know if the colonizations and extinctions are due to sampling error, sampling effort or reflect real events. In the longer data set, 84 species were seen in 5 years or less. Of 35 species detected in only 1 year, 24 species were recorded in the first 5 years and 11 in the next 10 years. Since sampling was most extensive in the first years, the encounters could reflect the sampling effort necessary to detect very rare species. Alternatively, observations of rare species may have declined because the reduced sampling missed species that arrive seasonally or call seasonally. Finally, we cannot discount misidentification of species rarely encountered.

The main conclusion from this analysis is that species richness is relatively stable in both datasets. Despite the high variability in sampling effort, RSR fluctuated by only 10% in the 1997 dataset and 3% in the 2005 dataset. The only possible climatic effect was possibly a spike in local extinction during exceptionally wet years followed by a spike in colonization. This effect was not seen in one of the wettest years (2003) and was not observed in the 2005 dataset for the 2006 wet year. Other than this potential anomaly, the bird community appears resilient. The stability of RSR supports the idea that Nyungwe may serve as a biodiversity refugia in times of climatic change as speculated by Picton-Phillips & Seimon (2010).

The high similarity of species composition between the 1997 and 2005 datasets is not surprising given that both datasets share a similar elevation gradient (1997 goes a bit higher) and are dominated by forest habitat. Most of the dissimilarity is due to addition of new habitats in the 2005 dataset. Cyamudongo Forest has only one unique species, the Ross' turaco.

Encounter Rates and Density Estimation: 1997 - 2011

We observed 193 species (non-flying observations only), in 121 genera and 43 families at least once during the 1997 - 2011 surveys. We used a cutoff of 5 years of nonzero data to estimate densities and relative abundance for species. We felt that 6 years of nonzero observations was a minimum for trend data and at 5 observations, we need a correlation of 0.90 to attain a trend with P=0.1 significance level. We calculated 940 density estimates for 78 species with at least 5 years of non-zero data and sufficient sample sizes for an average of 12.0 estimates per species (Appendix 1). Most density estimates were rated as good (72.3%) and medium (20.5%). Densities were examined for general time trends and time trends at low and high elevations. To evaluate whether encounter rates accurately tracked density, we calculated annual correlations between density and encounter rate. Annual correlations between density estimates and relative abundance indices (encounters/yr/point) ranged from 0.86 to 0.69 (Figure 23) with an average correlation of 0.78 and an overall correlation of 0.75. All correlations were highly significant and we felt confident to use encounter rates as a surrogate for density in examining trends in abundance by elevation and extending the inferences based on density to a broader set of species.

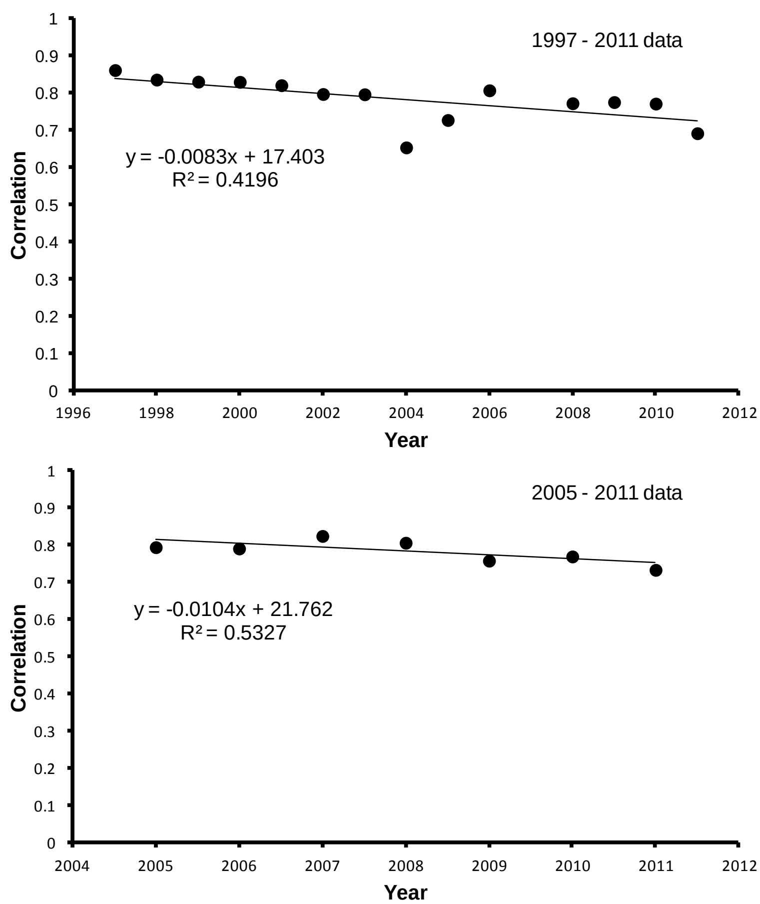


Figure 23. Annual correlation between estimated density and relative abundance index for 1997 - 2011 and 2005 - 2011 bird count data.

Table 12. Trends in bird density over time for the 1997 - 2011 dataset. The time trend is the slope of the linear regression for a given sample size (N) and P is the level of significance.

Group	Common Name	Genus/Species	All Data			Below 2,350 masl			Above 2,350 masl		
			Time trend	N	P	Time trend	N	P	Time trend	N	P
Cuckoo	Emerald Cuckoo	*Chrysococcyx cupreus*	**0.044**	**14**	**0.10**	**0.043**	**14**	**0.10**	No trend	1	NS
Large frugivore	Great Blue Turaco	*Corythaeola cristata*	**-0.359**	**14**	**0.05**	**-0.355**	**14**	**0.05**	-0.084	14	NS
Large frugivore	Ruwenzori turaco	*Tauraco johnstoni*	-0.253	14	NS	**-0.171**	**14**	**0.10**	0.054	14	NS
Large frugivore	Narina's Trogon	*Apaloderma vittatum*	**0.206**	**14**	**0.05**	**0.264**	**14**	**0.05**	0.055	13	NS
Babblers	Mountain Illadopsis	*Illadopsis pyrrhoptera*	**2.101**	**14**	**0.10**	**1.772**	**14**	**0.05**	**0.615**	**14**	**0.10**
Babblers	Grey-chested Illadopsis	*Kakamega poliothorax*	**-0.569**	**14**	**0.10**	-0.305	14	NS	**-0.184**	**14**	**0.10**
Babblers	Red-collared Mountain Babbler	*Kupeornis rufocinctus*	1.375	14	NS	0.013	14	NS	**-0.521**	**13**	**0.10**
Warblers	Grey Apalis	*Apalis cinerea*	**0.609**	**14**	**0.05**	**0.769**	**14**	**0.05**	**2.378**	**14**	**0.05**
Warblers	Montane Masked Apalis	*Apalis personata*	**5.296**	**14**	**0.10**	**5.428**	**14**	**0.05**	No Trend	0	NS
Warblers	Chestnut-throated Apalis	*Apalis porphyrolaema*	**-2.808**	**14**	**0.05**	**-1.577**	**14**	**0.05**	**-1.361**	**14**	**0.05**
Warblers	Black-faced Rufous Warbler	*Bathmocercus rufus*	**0.910**	**14**	**0.05**	**1.133**	**14**	**0.05**	No trend	4	NS
Warblers	Cinnamon Bracken Warbler	*Bradypterus cinnamomeus*	-1.647	14	NS	**-1.146**	**14**	**0.05**	-0.034	14	NS
Warblers	Grey-backed Camaroptera	*Camaroptera brachyura*	0.061	13	NS	**0.152**	**13**	**0.05**	No trend	0	NS
Warblers	Mountain Yellow Warbler	*Chloropeta similis*	-0.337	14	NS	**-0.214**	**11**	**0.05**	-0.044	14	NS
Warblers	Chubb's Cisticola	*Cisticola chubbi*	**-1.661**	**14**	**0.05**	**-1.099**	**14**	**0.05**	**-0.450**	**14**	**0.10**
Warblers	Brown Woodland Warbler	*Phylloscopus umbrovirens*	0.073	13	NS	No trend	0	NS	**0.152**	**13**	**0.05**
Warblers	Banded Prinia	*Prinia bairdii*	-1.811	14	NS	-1.061	14	NS	**-0.655**	**14**	**0.05**
Warblers	White-browed Crombec	*Sylvietta leucophrys*	**-0.320**	**14**	**0.05**	**-0.264**	**13**	**0.05**	-0.042	13	NS
Flycatchers	Yellow-eyed Black Flycatcher	*Melaenornis ardesiacus*	**1.041**	**14**	**0.05**	**1.443**	**14**	**0.05**	-0.005	12	NS
Flycatchers	White-eyed Slaty Flycatcher	*Melaenornis fischeri*	**0.286**	**14**	**0.10**	0.203	13	NS	0.078	13	NS
Flycatchers	Dusky Flycatcher	*Muscicapa adusta*	-0.111	14	NS	-0.120	14	NS	**0.311**	**14**	**0.10**
Flycatchers	Paradise Flycatcher	*Terpsiphone viridis*	**-0.505**	**14**	**0.10**	-0.281	14	NS	-0.007	14	NS
Flycatchers	White-bellied crested-flycatcher	*Trochocercus albiventris*	0.379	14	NS	**0.287**	**7**	**0.10**	-0.0447	7	NS
Flycatchers	Blue-mantled Crested Flycatcher	*Trochocercus cyanomelas*	0.280	13	NS	**0.569**	**13**	**0.05**	No trend	4	NS
White-eye	Yellow White-eye	*Zosterops senegalensis*	2.059	14	NS	1.480	14	NS	**1.291**	**14**	**0.10**
Bush-shrike	Brown-headed Tchagra	*Tchagra australis*	**-0.076**	**10**	**0.05**	**-0.070**	**10**	**0.05**	No trend	2	NS
Sunbirds	Ruwenzori double-collared sunbird	*Cinnyris stuhlmanni*	1.136	14	NS	0.882	13	NS	**0.472**	**11**	**0.10**
Sunbirds	Variable Sunbird	*Cinnyris venusta*	**1.177**	**14**	**0.05**	**0.930**	**13**	**0.05**	**0.471**	**11**	**0.10**
Sunbirds	Blue-headed Sunbird	*Cyanomitra alinae*	4.999	14	NS	**5.746**	**14**	**0.10**	**0.758**	**13**	**0.05**
Sunbirds	Olive Sunbird	*Cyanomitra olivacea*	**1.210**	**14**	**0.10**	1.106	14	NS	0.249	11	NS
Sunbirds	Collared Sunbird	*Hedydipna collaris*	**4.653**	**14**	**0.05**	**4.266**	**14**	**0.05**	**0.813**	**14**	**0.05**

Eighteen species had a significant ($P<0.05$) or moderate ($P<0.10$) time trend in density at all elevations (Table 12) indicating significant changes in abundance over time. The main groups include warblers (6 species), flycatchers (3 species) and sunbirds (3 species). Eleven species have increasing trends over time and 7 species have declining trends. Considering only the low elevation density trends (below 2,350 masl), 21 species had a significant or moderate time trend with 11 positive and 8 negative trends (Table 12). The main groups include warblers (9 species), large frugivores (3 species), flycatchers (3 species) and sunbirds (3 species). Flycatchers and sunbirds are consistently increasing at lower elevations, whereas turacos are declining and trogons are increasing. Among the warblers, trends are inconsistent with 5 species declining and 4 species increasing. At high elevations (above 2,350 masl) 9 species are increasing in density and 5 species are declining in density. Major groups include warblers (3 species declining, 2 species increasing), sunbirds (4 species, all increasing) and babblers (2 species declining, 1 increasing).

To evaluate the potential influence of climate change on elevational distribution we first classified 263 bird species by elevation distribution relative to the range of elevations within the park study area as: 1. Minimum elevation <1500, Max elevation <3000 (182 species); 2. Minimum elevation <1500, Maximum elevation >3000 (17 species); 3. Minimum elevation >1500, Maximum elevation <3000 (47 species), 4. Minimum elevation >1500, Maximum elevation >3000 (17 species). We hypothesized that: 1. Species whose elevation ranges spanned the elevation range of the study area would, on average, show no trend in mean elevation observed over time; 2. Species whose maximum elevation range was within the study area would show and increasing trend in elevation. We believed that species whose elevation range spanned to range of the study area would be very tolerant to climate change since they already are adapted to a broad spectrum of temperatures and rainfall. Species with maximum or minimum elevation within the range of the study area would be more likely to show a detectable shift in range. We regressed mean elevation of observations per species per year against time to assess these hypotheses. We assessed the time trend in elevation for 108 species, of which 92 species were in the a priori prediction list. Among 27 species for which no change in elevation distribution was predicted, 11 species showed declining trends in mean elevation, 3 species showed increasing trends in elevation, and 13 species showed no trend in elevation. The probability of 13 no changes in 27 trials with 3 potential outcomes is 0.04, whereas the probability of 11 declining species in 27 trials is 0.11. We conclude that there are significantly more species showing no change than would be expected for a random outcome. Among the 65 species for which increases in mean elevation of observations were predicted, 12 species showed declining trends, 22 species showed increasing trends, and 31 species no trends in elevation over time. The probability of 22 species showing an increasing trend in 65 trials is 0.10, whereas the probability of 31 species showing no trend in 65 trials is 0.006. We conclude that there is some little evidence to support a community-wide response by species that are expected to be sensitive to climate change.

Table 13. Trends in mean elevation of bird observations over time for the 1997 - 2011 dataset. The time trend is the slope of the linear regression for a given sample size (N years), P is the level of significance, and observations is the number of records for all years. Min(Elevation) is the shift in minimum elevation of observations between 1997-2001 data and 2006-2011 data. Max(Elevation) is the shift in maximum elevations between 1997-2001 data and 2006-2011. * indicates species with significant changes in abundance over time.

Group	Common name	Species	Time trend	N	P	min(Elevation)	max(Elevation)	Observations
Raptor	African goshawk	*Accipiter tachiro*	-19.96	11	0.10	6	-706	38
Pigeons	Lemon Dove	*Aplopelia larvata*	12.97	9	0.05	280	-160	21
Cuckoo	Black Cuckoo	*Cuculus clamosus*	17.79	11	0.10	36	300	38
Large frugivore	Narina's Trogon*	*Apaloderma vittatum*	-5.68	13	0.10	-17	-140	330
Large frugivore	Ruwenzori turaco*	*Tauraco johnstoni*	7.13	14	0.05	56	0	1899
Bee-eater	Eurasian Bee-eater	*Merops apiaster*	-32.11	10	0.05	-10	-70	488
Broadbill	African Broadbill	*Smithornis capensis*	-11.96	13	0.05	-35	-290	110
Woodpecker	Olive Woodpecker	*Dendropicos griseocephalus*	31.23	12	0.05	-56	270	49
Thrush	Red-throated Alethe	*Alethe poliophrys*	-8.53	13	0.05	5	-330	498
Thrush	Archer's Ground Robin	*Cossypha archeri*	9.17	13	0.05	39	0	1061
Thrush	White-starred Forest Robin	*Pogonocichla stellata*	11.43	13	0.05	112	-60	325
Warbler	Tawny-flanked Prinia	*Prinia subflava*	8.01	9	0.05	340	-160	43
Warblers	Grey Apalis*	*Apalis cinerea*	-4.28	13	0.05	-7	-300	663
Warblers	Cinnamon Bracken Warbler*	*Bradypterus cinnamomeus*	9.98	14	0.05	162	0	2456
Warblers	Grey-backed Camaroptera*	*Camaroptera brachyura*	13.88	12	0.05	49	90	50
Warblers	Mountain Yellow Warbler*	*Chloropeta similis*	8.03	13	0.05	500	-60	397
Warblers	Chubb's Cisticola*	*Cisticola chubbi*	4.86	13	0.05	0	-90	2608
Babbler	African Hill Babbler	*Pseudoalcipe abyssinica*	6.46	14	0.05	52	-80	1068
Bulbuls	Slender-billed Greenbul	*Andropadus gracilirostris*	-4.43	12	0.05	24	-140	323
Bush shrike	Tropical boubou	*Laniarius aethiopicus*	4.56	10	0.10	0	100	22
Bush shrike	Luhder's Bush Shrike	*Laniarius luehderi*	-7.79	13	0.05	79	-50	110
Flycatchers	Paradise Flycatcher	*Terpsiphone viridis*	-4.02	13	0.10	0	-380	803
Sunbird	Purple-breasted Sunbird	*Nectarinia purpureiventris*	9.43	13	0.05	57	-60	885

We then compared the average minimum elevation and average maximum elevation for the first 5 years of surveys to the last 5 years of surveys. Twenty three species showed significant changes in mean elevation over time (Table 13) with 9 species shifting downhill and 14 species shifting uphill. Warblers (6 species) and Thrushes (3 species) were the main bird groups. Trends range from a shift in observations of 4 m/year downhill to 31 m/year uphill. Eight species showed evidence of compression with minimum elevations shifting uphill and maximum elevations shifting downhill, and among these, 6 species shifted their mean distribution uphill and 2 species shifted their mean distribution downhill.

Several species show trends in both distribution and abundance. Among large frugivores, The Ruwenzori turaco is declining in abundance shifting distribution uphill, while the Narina's Trogon is increasing in abundance and shifting distribution downhill. Among the warblers, Grey apalis is increasing abundance and shifting distribution downhill, and Grey-backed camaroptera is increasing abundance and shifting distribution uphill. The Cinnamon bracken warbler, mountain yellow warbler and Chubb's cisticola are declining in abundance and shifting distributions uphill.

Encounter Rates and Density Estimation: 2005 - 2011

We observed 157 species (non-flying observations only), in 105 genera and 40 families at least once during the 2005-2011 surveys. We calculated 645 density estimates for 97 species with at least 5 years of non-zero data and sufficient sample sizes for an average of 6.7 estimates per species (Appendix 1). Most density estimates were rated as good (53.4%) or medium (25.4%). Densities were examined for time trends only, because we did not enough data to split between high and low elevations. Annual correlations between density estimates and relative abundance indices ranged from 0.73 to 0.82 (Figure 23) with an average annual correlation of 0.78 and an overall correlation of 0.76. All correlations were highly significant and we felt confident to use encounter rates as a surrogate for density in extending the examination of trends in abundance.

Table 14. Trends in bird density over time for the 2005 - 2011 dataset. The time trend is the slope of the linear regression for a given sample size (N) and P is the level of significance.

Group	Common name	Species	NonZero N	Time trend in RAI	P	Time trend in Density	P
Ibis	Hadada Ibis	Bostrichia hagedash	7	0.005	0.05	No trend	NS
Barbets	Yellow-rumped Tinkerbird	Pogoniulus bilineatus	7	-0.034	0.10	-4.794	0.05
Cuckoo	Emerald cuckoo	Chrysococcyx cupreus	7	0.005	0.05	0.271	0.10
Granivores	Streaky Seed-eater	Serinus striolatus	6	-0.017	0.05	-6.307	0.10
Flycatchers	Chin-spot Batis	Batis molitor	5	No trend	NS	0.811	0.05
Large Frugivores	Ruwenzori Turaco	Tauraco johnstoni	7	0.020	0.10	No trend	NS
Wood hoopoe	White-headed Wood Hoopoe	Phoeniculus bollei	7	No trend	NS	-6.597	0.10
Bulbul	Placid Geenbul	Phyllastrephus placidus	7	0.014	0.05	No trend	NS
Bulbul	Common/Yellow-vented Bulbul	Pycnonotus barbatus	7	No trend	NS	-3.996	0.10
Starlings	Waller's Chestnut-winged Starling	Onychognathus Walleri	7	No trend	NS	-3.800	0.10
Starlings	Montane Oriole	Oriolus percivali	7	-0.010	0.10	-1.181	0.05
Warbler	Cinnamon bracken warbler	Bradypterus cinnamomeus	7	0.030	0.10	No trend	NS
Warbler	Red-faced Woodland Warbler	Phylloscopus laetus	7	0.011	0.10	No trend	NS
Babbler	Mountain Illadopsis	Illadopsis pyrrhoptera	7	0.014	0.05	Decline	NS
Babbler	African Hill Babbler	Pseudoalcipe abyssinica	7	No trend	NS	-1.786	0.10
Thrush	White-starred Forest Robin	Pogonocichla stellata	7	0.005	0.10	No trend	NS
Thrush	Equatorial Akalat	Sheppardia aequatorialis	7	0.001	0.10	No trend	NS

Nine species had significant (3 species) or moderate (6 species) trends in abundance over time and 8 additional species had significant (3 species) or moderate (5 species) trends in relative abundance (Table 14). Most abundance trends were declining over time (7 species), whereas all trends in relative abundance were increasing. Five species groups contained 2 species; Thrushes, warblers, bulbul, babbler, and starling. The relative lack of significant trends in the 2005 - 2011 data set reflects the small sample size (7 years) and high variability of estimates within species.

We conclude that the bird community in Nyungwe National Park has remained relatively stable between 1997 and 2011. Community composition has stayed stable over time in both data sets with the expected exception of high turnover among the rare species due to sampling error. Of the 98 species for which we calculated densities, 14 species are declining and 13 species are increasing, and the remaining species show no pronounced trends in density.

DISCUSSION: Birds

Species richness and community dynamics

Species richness and community composition appear to be stable between 1997 and 2011 in Nyungwe NP. Approximately 25% of species are so rare that they only are detected once or twice in the 1997-2011 dataset, whereas only 8% of species in 2005-2011 dataset were detected twice or less. Species richness is very stable over time with annual rates of change of only 1 - 3% on average, and community similarity between years averaging 86% and 89% for the 2 datasets. The similarity in community composition between the 1997 and 2005 datasets was also high at 80 – 86% with most differences attributed to the addition of new habitats in 2005. Much of the turnover is likely due to sampling error involving rare species and low sampling effort in later years.

Trends in density, relative abundance, and elevation distribution

There were few significant time trends in bird species. Of 108 species, approximately half had sufficient data to calculate time trends between 1997 and 2011. Of these, 10 species increased in density over time and 6 species declined. An additional 7 species showed significant changes in relative abundance with 2 species declining and 5 species increasing. There was no strong taxonomic affinity among species showing significant trends and species ranged from variable sunbird to crowned eagle.

At elevations below 2,350 masl, 10 species, mostly sunbirds and warblers, displayed increasing density trends and six species showed declines. At elevations above 2350 masl, 7 species, mostly sunbirds and warblers, displayed increasing density trends and 6 species showed declining trends. In general, however, there is no consistent, community-wide trend in distribution of observations by elevations over time. Of 108 species examined, mean elevation was declining for 50 and increasing for 58 species. Fourteen of 23 species had significant ($P \leq 0.10$) increasing trends in elevation, and 9 had significant declining trends. A test of a priori hypotheses about species responding to climate change by shifting elevation range showed that species with no expected change and species with expected increase in elevation range showed little evidence of change.

Lack of change is often difficult to explain, and a mixture of no change, increasing elevation range and decreasing elevation range is even harder to explain. Perhaps the strongest signal in the data, is that most increases in density (6 species) and relative abundance (6 species) are small bodied warblers, tits and sunbirds. These species might logically be considered the early responders to climate change since small changes in temperatures are likely to have larger thermal implications for small-bodied birds. More research is needed, however to confirm this speculation.

Albertine Rift Endemics

We estimated density trends for 13 Albertine rift endemic species and relative abundance trends for an additional 2 species. Yellow-eyed black flycatcher and Blue-throated sunbird have an increasing trend at lower elevations ($P \leq 0.10$), and show no shifts in elevation. Ruwenzori Turacos are declining at lower elevations ($P \leq 0.10$) at lower elevations and shifting their elevation range upward. The red-collared mountain Babbler is declining at higher elevations ($P \leq 0.10$) and its distribution appears to be heading downslope. The Stripe-breasted tit, Strange weaver and Grauer's warbler all show increasing trends in relative abundance, but no distributional shifts. Other Albertine Rift Endemic species showing distributional shifts upward include Purple-breasted sunbird, Archer's ground Robin. Species showing distributional shifts toward lower elevations include the Short-tailed warbler and Red-throated Alethe. Again, there is no strong pattern in trends in abundance of Albertine Rift Endemics.

Picton-Phillipps and Seimon (2010) and Chao et al (2010) suggest that Nyungwe might be considered a climate change refuge, because, as lower elevations become hotter, climatic conditions in the montane forests of Nyungwe should remain favorable for most species. The high mean elevations, and increased rainfall are expected to counteract the evaporative loss due to higher temperatures expected at lower elevations. The lack of trends in elevation for most bird species supports this speculation.

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Appendix 1. Mean density of bird species in 1997 - 2011 and 2005 - 2011 datasets. Full results for data analyses (mean and median estimates of density plus standard deviations) are available on request.

		2005 - 2011 Data							1997 -2011 Data													
Common Name	Scientific name	2005	2006	2007	2008	2009	2010	2011	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2008	2009	2010	2011
Red-throated Alethe	Alethe poliophrys	10.822	1.453	14.048	3.277	11.934	7.261	13.161	17.833	20.864	20.408	26.074	10.206	19.840	27.507	16.361	14.470	9.804	31.768	27.011	16.514	13.795
Slender-billed Greenbul	Andropadus gracilirostris	7.992	10.423	18.950	7.901	10.689	7.463	8.918	7.721	4.459	5.199	3.435	3.263	14.171	7.385	4.086	1.677	7.119	3.987	5.758	4.418	
Yellow-whiskered Greenbul	Andropadus latirostris	171.847	150.643	137.496	96.960	168.640	113.981	95.053	117.589	162.184	125.604	104.404	103.011	85.651	180.633	96.623	176.979	187.761	33.059	314.019	111.465	109.812
Mountain greenbul	Andropadus nigriceps	26.768	25.005	15.146	17.216	25.942	8.482	16.976	85.585	82.222	82.821	56.882	38.409	66.893	84.204	109.905	98.767	67.965		101.777	71.585	55.411
Grey Apalis	Apalis cinerea	21.938	17.768	50.771	7.425	15.237	3.322	21.938	9.599	15.556	9.497	5.980	4.842	9.759	18.531	16.652	12.548	16.547	18.060	13.879	21.135	13.579
Black-throated Apalis	Apalis jacksoni	73.764	6.497	25.635	25.612	13.800	11.797	17.768	27.762	20.924	19.069	14.358	7.761	17.667	22.286	16.114	16.896	23.812	25.092	18.215	28.746	15.862
Montane Masked Apalis	Apalis personata	43.460	42.168	94.037	54.677	71.601	40.571	50.771	69.340	108.724	75.225	156.094	106.831	146.569	191.613	133.961	141.102	151.568	227.261	183.667	160.220	103.337
Chestnut-throated Apalis	Apalis porphyrolaema	7.434	9.771	3.161	13.305	11.019	5.697	7.425	58.711	68.411	43.127	24.629	22.834	29.193	40.946	22.138	22.558	17.668	23.481	14.461	21.542	14.300
Collared apalis	Apalis ruwenzorii	16.136	19.158	23.536	26.425	22.001	23.077	15.237	126.756	120.139	64.233	60.915	51.516	68.244	108.530	80.837	88.752	90.945	72.311	109.901	44.181	48.674
Narina's Trogon	Apaloderma narina	3.886	1.595	2.237	2.168	6.644	1.129	3.322	1.711	0.622	0.334	2.099	2.037	2.039	1.386	1.697	1.080	2.904	1.896	3.300	0.845	1.246
Bar-tailed Trogon	Apaloderma vittatum	12.775	4.829	7.263	2.596	7.673	8.602	8.313	2.470	1.866	1.950	1.836	1.401	3.399	4.159	1.697	3.565	3.872	6.636	3.850	4.791	2.991
Lemon Dove	Aplopelia larvata	0.775		0.606	0.322	0.409		0.259	0.174	0.140			0.113	0.596		0.131	0.385		0.360		0.138	0.162
Black-faced Rufous Warbler	Bathmocercus rufus	21.292	20.316	17.084	15.067	25.202	16.429	16.464	2.322	4.980	4.797	7.708	9.040	8.760	17.776	17.368	17.254	23.650	17.373	10.505	16.661	12.330
Rwenzori Batis	Batis diops	23.976	23.170	12.444	20.215	33.386	13.790	26.165	37.661	44.530	24.586	32.571	8.899	18.336	43.317	48.984	33.842	28.749	51.776	32.748	32.466	33.186
Chin-spot Batis	Batis molitor	3.996	2.896		4.717		7.258	8.120														
Cinnamon Bracken Warbler	Bradypterus cinnamomeus	64.183	73.187	102.939	107.067	152.144	78.590	73.764	61.133	70.433	36.129	43.253	28.969	33.655	53.891	36.043	37.811	33.728	71.456	32.921	28.216	16.683
Grauer's Rush Warbler	Bradypterus graueri	10.736	10.748	4.482	3.947	5.813	8.860	6.497														
Black and White Casqued Hornbill	Bycanistes subcylindricus	3.641	2.480	3.531	3.834	1.410	4.380	6.931	2.908	3.316	1.594	2.953	3.275	0.889	2.258	2.874	1.015	2.044	5.653	3.706	1.307	1.234
Grey-backed Camaroptera	Camaroptera brachyura	18.858	5.944	7.822	6.491	14.067	12.513	6.846	0.245	0.250	1.161	2.680	0.627	3.079	2.426	2.794	2.141	2.279		2.199	2.624	1.178
Barred Long-tailed Cuckoo	Cercococcyx montanus	15.847	15.380	14.727	11.408	4.640	7.449	13.754	5.867	6.780	2.175	9.303	7.938	9.028	11.884	6.050	9.640	7.481	10.638	3.386	4.312	8.447
Green Coucal	Ceuthmochares aereus																					
Mountain Yellow Warbler	Chloropeta similis	3.643	9.671	9.938	11.168	20.883	7.935	6.692	9.542	13.500	10.963	7.504	3.137	12.315	8.317	3.592	8.565	5.926	5.235	10.997	6.997	3.142
Emerald Cuckoo	Chrysococcyx cupreus	0.641	0.447	0.203	1.765	0.868	2.150	1.817	0.479	0.110	0.228	0.274	1.081	0.079	0.548	0.111	0.831	1.136	0.848	1.129	0.192	1.030
Klaas' Cuckoo	Chrysococcyx klaas								0.167		0.173	0.091	0.077				0.083				0.096	0.309
Sharpe's Starling	Cinnyricinclus sharpii	13.999	8.660	4.248	3.606	13.908	3.815	3.635														
regal sunbird	Cinnyris regia	41.190	61.507	29.046	30.760	23.844	42.277	21.805	139.926	183.033	139.774	136.562	133.812	145.995	261.510	275.738	209.441	166.553	162.323	118.690	205.043	229.383
Ruwenzori double-collared sunbird	Cinnyris stuhlmanni	25.450	23.584	18.346	28.314	32.506	20.838		13.481	9.751	25.760	11.219	11.148	12.249	15.087	23.786	18.212	39.717	4.387	19.782	45.300	23.196
Variable Sunbird	Cinnyris venusta		36.070	4.587	19.820	21.671	17.365	18.822	7.641	4.469	7.825	4.207	5.574	5.249	13.830	27.750	21.248	20.499	4.387	27.694	21.458	15.464
Chubb's Cisticola	Cisticola chubbi	40.065	49.970	51.712	38.717	58.094	37.009	13.669	40.766	52.032	31.730	20.289	23.464	28.320	31.406	19.577	22.117	31.579	16.880	22.393	18.194	13.283
Olive Pigeon	Columba arquatrix	0.387	1.796	4.729	3.218	3.276	0.303	0.777	2.981	2.129	4.722	0.604	3.517	0.795	7.737	0.523	3.206	1.699	0.360	4.040	0.138	0.971
Great Blue Turaco	Corythaeola cristata	2.800	2.569	3.261	1.168	1.179	1.567	2.629	12.943	8.873	4.960	4.201	5.219	4.259	6.726	2.382	4.416	3.071	5.797	2.453	3.764	4.971
Archer's Ground Robin	Cossypha archeri	5.090	10.389	4.286	5.318	1.278	5.144	7.591	6.277	15.387	24.625	21.361	21.185	24.509	35.653	24.956	25.575	30.259	12.133	49.518	13.589	18.545
Black Cuckoo	Cuculus clamosus	1.153	0.335	0.406	0.588	1.085	0.586	1.677	0.291		0.135		0.541	0.317	0.457	0.222		0.284	0.212	1.129	0.192	0.206
Red-chested Cuckoo	Cuculus solitarius		0.112	0.406	0.490	1.085	0.391	0.280	0.060	0.083					0.274					0.376	0.192	0.103
Blue-headed Sunbird	Cyanomitra alinae	33.288	25.030	26.726	12.316	82.070	18.157	31.290	29.590	40.256	93.316	92.371	66.782	70.108	158.403	195.115	89.262	131.836	71.904	187.180	88.123	103.734
Olive Sunbird	Cyanomitra OLivacea	33.933	15.260	12.231	14.157	86.684		45.711	1.279	9.345	19.138	29.450	21.181	22.747	32.689	31.714	36.424	28.186	39.484	7.913	30.995	28.351
White-tailed Blue flycatcher	Eliminia albicauda								1.321	1.157									2.396	3.259		0.855
Yellow-bellied Wattle-eye	Dyaphorophyia concreta	2.997	0.724	2.705	2.022		3.629	1.805														
Northern Puffback	Dryoscopus gambensis	1.515	0.147	0.458	0.797	3.486	0.423	3.500	6.403	2.768	4.556	5.563	0.467	2.199	10.867	1.880	4.271	1.969	4.942	0.396	3.735	2.219

		2005 - 2011 Data							1997 -2011 Data													
Species	Scientific name	2005	2006	2007	2008	2009	2010	2011	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2008	2009	2010	2011
Black-headed Waxbill	Estrilda atricapilla		0.278	0.976	1.351		1.130	0.507														
Grauer's Warbler	Graueria vittata	4.413	10.200	8.075	6.913	10.549	10.170	5.594	7.718	6.128	4.124	7.765	6.752	7.202	12.009	7.937	12.042	8.484	4.588	11.428	9.190	9.113
Grey-throated Barbet	Gymnobucco bonapartei	30.535	14.936	27.956	14.138	21.143	13.750	14.253														
Collared Sunbird	Hedydipna collaris	29.691	33.295	42.808	38.224	65.013	41.676	43.022	6.257	0.784	13.846	24.245	12.603	25.317	48.127	22.846	48.272	47.034	95.426	41.155	64.044	55.291
Short-tailed/Neumann's Warbler	Hemitesia neumanni	18.250	10.773	10.057	9.087	11.509	17.987	11.248		26.099	15.539	25.998	21.579	20.084	33.245	24.954	26.051	30.982	31.941	28.010	18.619	22.159
Mountain Illadopsis	Illadopsis pyrrhoptera	14.830	12.630	15.231	12.008	13.870	13.630	12.530	4.738	5.495	26.975	22.948	18.508	18.763	26.375	9.965	11.845	15.078	19.845	74.931	37.539	27.196
White-tailed Blue flycatcher	Eliminia albicauda								1.321	1.157									2.396	3.259		0.855
Yellow-bellied Wattle-eye	Dyaphorophyia concreta	2.997	0.724	2.705	2.022		3.629	1.805														
Black-headed Waxbill	Estrilda atricapilla		0.278	0.976	1.351		1.130	0.507														
Grauer's Warbler	Graueria vittata	4.413	10.200	8.075	6.913	10.549	10.170	5.594	7.718	6.128	4.124	7.765	6.752	7.202	12.009	7.937	12.042	8.484	4.588	11.428	9.190	9.113
Grey-throated Barbet	Gymnobucco bonapartei	30.535	14.936	27.956	14.138	21.143	13.750	14.253														
Collared Sunbird	Hedydipna collaris	29.691	33.295	42.808	38.224	65.013	41.676	43.022	6.257	0.784	13.846	24.245	12.603	25.317	48.127	22.846	48.272	47.034	95.426	41.155	64.044	55.291
Short-tailed/Neumann's Warbler	Hemitesia neumanni	18.250	10.773	10.057	9.087	11.509	17.987	11.248		26.099	15.539	25.998	21.579	20.084	33.245	24.954	26.051	30.982	31.941	28.010	18.619	22.159
Mountain Illadopsis	Illadopsis pyrrhoptera	14.830	12.630	15.231	12.008	13.870	13.630	12.530	4.738	5.495	26.975	22.948	18.508	18.763	26.375	9.965	11.845	15.078	19.845	74.931	37.539	27.196
Grey-chested Illadopsis	Kakamega poliothorax	10.073	5.250	6.690	8.526	27.017	8.041	3.331	15.747	14.904	9.489	10.865	11.161	11.147	24.836	16.257	14.848	13.052	5.994	9.464	4.272	6.211
Red-collared Mountain Babbler	Kupeornis rufocinctus	3.358	1.458	1.968	2.984	3.860	5.361	0.769	15.898	18.426	17.316	7.873	6.815	14.137	5.502	12.748	9.306	13.222	5.198	8.273	11.595	78.599
Tropical Boubou	Laniarius aethiopicus	1.212	0.737	0.458	0.266	1.162	0.141	0.583	0.064			0.654	0.187		1.509	0.289	0.407	0.492	0.549	0.396		0.403
Luhder's Bush Shrike	Laniarius luehderi		4.272	4.735	2.921	7.552	3.670	5.639	0.300	0.540	0.268	3.272	0.841	1.553	2.717	0.868	1.220	1.477	0.549	1.189	2.668	1.412
Montane Sooty Boubou	Laniarius poensis	23.671	10.221	10.932	8.482	15.673	9.897	8.990	40.475	36.613	23.181	32.519	40.514	35.642	49.547	54.760	44.690	29.351	26.477	20.657	21.905	23.801
Doherty's Bush Shrike	Malaconotus dohertyi	15.343	11.805	7.868	7.727	12.434	9.983	9.635	2.772	5.402	2.237	5.235	1.588	2.458	7.245	3.182	5.695	1.600	6.590	0.198	4.269	2.017
Many-coloured Bush Shrike	Malaconotus multicolor	1.515	0.147	0.458	0.664	1.162																
Yellow-eyed Black Flycatcher	Melaenornis ardesiacus	18.981	11.585	5.410	8.760	11.783	8.710	14.436	6.460	17.645	4.877	10.584	19.493	17.447	16.953	25.599	19.201	21.617	19.168	26.070	31.760	13.681
White-eyed Slaty Flycatcher	Melaenornis fischeri	9.990	3.620	2.705	5.391		5.806	3.609	0.718	2.603	7.575	3.900	4.641	4.105	3.989	4.923	3.840	4.323	11.980	3.259	6.352	6.841
Eurasian Bee-eater	Merops apiaster								2.630	6.781	2.970	8.058	7.627	4.316	13.233	6.339	7.438	6.918			0.984	
Cinnamon-chested Bee-eater	Merops oreobates								0.642	5.256		2.179	3.813	0.369	1.103	9.440	0.565	2.965			3.935	1.760
Dusky Flycatcher	Muscicapa adusta	6.993	5.792	3.787	2.695	1.964	7.984	7.218	30.802	19.380	17.266	3.900	10.211	13.855	13.462	14.768	13.825	15.564	26.356	22.811	19.056	6.841
Ross's Turaco	Musophaga rossae	17.161	4.698	13.802	8.478	7.437	11.632	9.241														
Purple-breasted Sunbird	Nectarinia purpureiventris	25.450	30.521	12.231	24.067		26.047	8.067	12.736	27.164	35.082	12.550	28.563	22.943	40.107	23.537	20.184	62.867	12.417		23.759	16.991
White-tailed Ant Thrush	Neocossyphus poensis	0.601	1.453	1.653	2.185		0.484	2.078														
Grey-headed Negrofinch	Nigrita canicapilla	1.078	2.501	2.929	2.702	1.675	2.825	3.548														
Slender-billed Chestnut-winged Starling	Onychognathus tenuirostris	5.000	1.732	4.248			2.861	0.727														
Waller's Chestnut-winged Starling	Onychognathus walleri	27.625	39.275	21.109	16.171	4.768	13.379	14.871	47.889	19.733	32.032	10.489	31.385	9.297	25.998	33.398	26.985	41.326	43.271	7.618	12.593	13.325
Montane Oriole	Oriolus percivali	13.334	10.868	8.847	8.185	6.462	8.341	4.792														
White-headed Wood Hoopoe	Phoeniculus bollei	66.708	28.742	23.991	14.453	8.616	21.049	15.388	23.708	17.117	7.851	14.338	12.381	13.914	19.485	30.253	14.251	10.362	22.153	3.345	20.084	7.164
Yellow-streaked Greenbul	Phyllastrephus flavostriatus	27.589	38.448	48.544	28.311	93.707	31.072	19.457	72.299	88.909	50.202	56.290	55.664	44.645	100.289	62.024	44.457	63.722	80.851	92.861	74.210	66.269
Placid Geenbul	Phyllastrephus placidus	4.995	1.303	21.055	21.446	32.067	19.404	22.295	5.760	0.478	2.313		0.466	0.443			0.335		0.664	1.152	0.491	0.399
Red-faced Woodland Warbler	Phylloscopus laetus	32.064	36.682	28.386	46.290	36.433	23.663	35.850	159.271	189.999	115.085	93.451	113.882	110.544	133.727	101.552	91.134	87.891	127.126	169.319	127.117	102.728
Brown Woodland Warbler	Phylloscopus umbrovirens	4.667	20.176	24.410	28.383	38.788	30.749	14.519	1.034	2.875	1.551	2.680	1.255	2.199	1.733	1.197	2.998	2.279		4.399	3.499	0.786
Strange Weaver	Ploceus alienus	15.247	4.432	5.357	2.462	12.835	15.345	10.181														
Stuhlmann's/Baglafecht Weaver	Ploceus baglafecht	3.518	5.910	5.952	4.432	2.852		2.545														

		2005 - 2011 Data							1997 -2011 Data													
Species	Scientific name	2005	2006	2007	2008	2009	2010	2011	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2008	2009	2010	2011
Yellow-rumped Tinkerbird	Pogoniulus bilineatus	31.875	46.063	38.613	24.794	15.658	14.418	15.880	11.328	18.058	11.796	8.919	11.759	7.434	21.377	10.851	21.697	11.077	3.961	31.837	30.199	19.909
White-starred Forest Robin	Pogonocichla stellata	2.405	6.782	5.784	9.286	13.639	5.809	9.005														
Banded Prinia	Prinia bairdii	36.803	30.182	45.003	44.550	26.104	17.044	26.510	50.879	78.330	30.738	41.541	37.662	7.434	66.431	34.592	29.944	48.525	36.380	29.732	22.544	25.495
Tawny-flanked Prinia	Prinia subflava	13.383	4.458	2.794	2.596	5.115	5.474	3.423	2.573	1.000		0.536	2.196		1.040	2.794	1.713			2.199	1.749	
Black saw-wing	Psalidoprocne holomelas		5.320	3.541	27.102		3.788	19.744	17.993	35.281	15.962	27.195	1.547	79.385	63.317	89.216	3.020	19.506			6.350	
African Hill Babbler	Pseudoalcipe abyssinica	18.689	12.622	4.166	8.307	4.431	5.696	6.547	8.265	15.167	19.042	15.712	24.513	22.869	37.915	27.029	28.747	22.740	8.378	22.184	16.024	11.340
Common/Yellow-vented Bulbul	Pycnonotus barbatus	41.566	29.941	15.441	17.598	21.514	21.068	8.163	9.016	8.759	4.809	4.723	6.992	7.528	12.133	12.711	8.049	8.899	8.638	5.758	7.854	4.789
Stonechat	Saxicola torquata	7.215	1.453	12.395	6.009	5.114	2.420	2.078														
African Citril	Serinus citrinelloides	5.133	23.027	31.158	10.839	5.787	21.676	97.711														
Streaky Seed-eater	Serinus striolatus	50.721	25.980	21.066	27.170	7.695	20.455	0.000														
Equatorial Akalat	Sheppardia aequatorialis	3.607	3.391	4.958	3.824	3.410	2.905	4.849														
African Broadbill	Smithornis capensis	2.516	3.335	6.835	2.702	2.513	5.649	3.548														
Red-eyed Dove	Streptopelia semitorquata								0.368	0.105		0.242	0.113					0.212				
White-browed Crombec	Sylvietta leucophrys	1.825	1.857	0.559	1.298	5.115	3.910	1.467	8.905	6.750	5.875	6.432	3.764	6.597	3.119	3.193	2.570	2.735	6.543	2.199	4.373	1.964
Ruwenzori turaco	Tauraco johnstoni	4.665	7.705	5.453	3.216	10.816	7.896	6.883	11.244	8.768	15.899	12.612	15.594	16.982	22.890	10.852	16.356	14.705	11.258	9.538	10.547	7.873
Black-billed Turaco	Tauraco schuetti	4.984	4.139	5.614	2.635	6.101	3.343	1.839														
Brown-headed Tchagra	Tchagra australis								1.691	0.675	0.827	0.982	0.280	0.259		0.145	0.407		0.549	0.198		
Paradise Flycatcher	Terpsiphone viridis	23.976		8.116	14.825	19.639	17.419	18.045	20.961	21.772	11.291	19.915	20.924	15.759	20.191	15.595	19.526	13.909	10.711	22.350	15.107	6.942
Crowned Hornbill	Tockus alboterminatus	1.081	0.661	1.173	1.003	4.033	0.000	0.000														
African green pigeon	Treron calva	1.679	2.155	0.364	1.931	0.409	0.152	0.777	0.171	0.244	0.380	0.604	0.454	0.497	1.517	1.178	0.898	2.337	1.081	0.253	0.275	0.162
White-bellied Crested Flycatcher	Trochocercus albiventris	7.992	2.896	2.705	10.781	9.819	5.081	10.827	10.033	8.967	8.360	6.128	13.924	11.802	11.468	11.815	3.072	3.459	19.168	6.517	17.468	16.246
White-tailed Crested Flycatcher	Trochocercus albonotatus								0.398	2.025		1.114						6.053		6.517	1.588	
Blue-mantled crested/Crested Flycatcher	Trochocercus cyanomelas	5.994	4.344	2.164	1.348	5.892	5.081	9.023	3.278	5.207	0.400	4.457	0.928	4.618	4.487	4.923	9.985	11.241		3.259	11.116	5.130
Olive thrush	Turdus olivaceus	7.076	5.703	6.944	2.565	4.233	7.496	7.732														
Tambourine Dove	Turtur tympanistria	15.629	9.065	17.206	4.736	9.320	6.728	10.094	2.331	4.481	1.808	1.177	3.683	4.986	7.597	1.829	8.097	2.805	1.229	1.206	0.855	2.839
Kivu Ground Thrush	Zoothera tanganjicae	4.208	2.907	2.479	1.092	3.410	1.936	0.693														
Yellow White-eye	Zosterops senegalensis	32.218	43.499	48.230	24.810	79.673	83.281	33.353	77.070	72.731	63.222	45.277	36.134	77.289	85.747	70.420	94.159	64.937	119.499	77.185	99.923	66.568